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Cadaver decomposition in terrestrial ecosystems

David O. Carter · David Yellowlees · Mark Tibbett

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Abstract A dead mammal (i.e. cadaver) is a high quality resource (narrow carbon:nitrogen ratio, high water content) that releases an intense, localised pulse of carbon and nutrients into the soil upon decomposition. Despite the fact that as much as 5,000 kg of cadaver can be introduced to a square kilometre of terrestrial ecosystem each year, cadaver decomposition remains a neglected microsite. Here we review the processes associated with the introduction of cadaver-derived carbon and nutrients into soil from forensic and ecological settings to show that cadaver decomposition can have a greater, albeit localised, effect on belowground ecology than plant and faecal resources. Cadaveric materials are rapidly introduced to belowground floral and faunal communities, which results in the formation of a highly concentrated island of fertility, or cadaver decomposition island (CDI). CDIs are associated with increased soil microbial biomass, microbial activity (C mineralisation)

and nematode abundance. Each CDI is an ephemeral natural disturbance that, in addition to releasing energy and nutrients to the wider ecosystem, acts as a hub by receiving these materials in the form of dead insects, exuvia and puparia, faecal matter (from scavengers, grazers and predators) and feathers (from avian scavengers and predators). As such, CDIs contribute to landscape heterogeneity. Furthermore, CDIs are a specialised habitat for a number of flies, beetles and pioneer vegetation, which enhances biodiversity in terrestrial ecosystems.

Keywords Mammal · Carbon cycle · Nutrient cycle · Forensic taphonomy · Scavenging · Biodiversity · Landscape heterogeneity · Postputrefaction fungi

Introduction

It is estimated that approximately 99% of the organic resources that undergo decomposition in a terrestrial ecosystem are plant-derived (e.g. leaf litter, root exudates, stems) or faecal matter (Swift et al. 1979). As a consequence, the breakdown of these materials has received a vast amount of attention (e.g. Aarons et al. 2004; Bjornlund and Christensen 2005). In contrast, the decomposition of dead mammals (i.e. cadavers) has long been a neglected microsite (Allee et al. 1949). This is in spite of the fact that a large number of mammals die from causes other than predation and leave their cadavers to decompose and nutrients to be recycled. In a Neotropical rainforest (Barro Colorado Island, Panama) (Eisenberg and Thorington Jr. 1973), 5,000 kg of mammal biomass per km² is associated

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with 750 kg of cadavers per year per km² (Houston 1985). The average annual bison (*Bos bison* L.) biomass in 988 ha of North American tallgrass prairie (Konza Prairie, Kansas, USA) from 1998 to 2004 was 92,432 kg (E.G. Towne, personal communication). An average mortality rate of 5.6% resulted in an annual bison cadaver input of approximately 5,000 kg and shows that cadaveric resources might represent more than 1% of the organic matter input in some terrestrial ecosystems.

Considering that each cadaver is approximately 20% carbon and acts as a specialised habitat for several organisms, cadaver decomposition is likely an important ecosystem process. It is therefore surprising that little is understood about the fate of cadaver-derived carbon and nutrients (e.g. nitrogen, phosphorus) (Putman 1978b; Vass et al. 1992; Hopkins et al. 2000; Towne 2000; Carter 2005) and cadaver components (e.g. bone, skeletal muscle tissue) (Child 1995; Aturaliya and Lukasewycz 1999; Carter and Tibbett 2006), particularly since carbon sequestration (Janzen 2006), carbon cycle modelling (Fang et al. 2005), soil organic matter formation (Moran et al. 2005) and the relationships between biodiversity and ecosystem function (McCann 2000; Fitter et al. 2005) are at the forefront of ecological research.

Much research into cadaver decomposition is done under the guise of forensic taphonomy. Taphonomy, originally a branch of palaeontology, was developed to understand the ecology of a decomposition site, how site ecology changes upon the introduction of plant or animal remains and, in turn, how site ecology affects the decomposition of these materials (Efremov 1940). In recent years, these goals were incorporated by forensic science to understand the decomposition of human cadavers (Rodriguez and Bass 1983; Spennemann and Franke 1995; Carter and Tibbett 2006), to provide a basis on which to estimate postmortem and/or postburial interval (Willey and Snyder 1989; Vass et al. 1992; Higley and Haskell 2001; Tibbett et al. 2004; Megyesi et al. 2005), to assist in the determination of cause and manner of death (Nuorteva 1977; Crist et al. 1997; Haglund and Sorg 1997) and to aid in the location of clandestine graves (Rodriguez and Bass 1985; France et al. 1992; Hunter 1994; France et al. 1997; Carter and Tibbett 2003). These goals are achieved through the study of the factors that influence cadaver decomposition (e.g. temperature, moisture, insect activity). These studies have also provided insight into the belowground ecology of cadaver breakdown.

The aim of the current work is to review the fundamental processes associated with the formation and ecology of gravesoil. We define gravesoil as any soil that is associated with cadaver decomposition, regardless of the species of mammal or whether decomposition takes place on or in the soil. This definition is based on the original aim of

taphonomy to understand the processes associated with the fossilisation of animal remains (Efremov 1940). Because gravesoil represents a linkage between aboveground and belowground ecology, this paper will review the relationships between gravesoils, intrinsic cadaver decomposition processes (autolysis, putrefaction), aboveground insect activity and scavenger activity. As a consequence, more fundamental work can be found on autolysis and putrefaction (Evans 1963b; Coe 1973; Clark et al. 1997; Gill-King 1997; Vass et al. 2002), cadaver associated insect activity (Schoenly and Reid 1987; Campobasso et al. 2001; Amendt et al. 2004) and scavenger activity (Haynes 1980; DeVault et al. 2003, 2004).

The formation of gravesoil

Although soil microbial biomass is recognised as ‘the eye of the needle’ (Jenkinson 1977) through which all organic material eventually passes, little work has focused on cadaver decomposition, belowground ecology and microbiology (Bornemissza 1957; Putman 1978b; Sagara 1995; Hopkins et al. 2000; Tibbett and Carter 2003). Advances in the understanding of gravesoils are primarily empirical observations (Illingworth 1926; Mant 1950; Evans 1963b; Morovic-Budak 1965; Sagara 1976; Micozzi 1991; Dent et al. 2004) or made during the study of insect and/or scavenger activity (Bornemissza 1957; Reed 1958; Payne 1965; Payne et al. 1968; Rodriguez and Bass 1985; DeVault et al. 2003). These observations and studies showed that introduction of cadaveric material into the soil is primarily regulated by the activity of insects and scavengers and the mass of the cadaver.

Insects, scavengers and microbes compete for cadaveric resources. Insects can consume a cadaver before a scavenger has utilised it (Putman 1978a; DeVault et al. 2004) and microorganisms can release repellent toxins, such as botulin toxin (Janzen 1977). However, scavengers were observed to consume 35% to 75% of the cadavers in terrestrial ecosystems (DeVault et al. 2003). When insects and microbes are less active (such as during winter) scavenger success can approach 100% (Putman 1983). Smaller cadavers (i.e. rodents, juveniles) tend to be consumed *ex situ* so that the amount of cadaveric material entering the soil might be negligible (Putman 1983). Adult or large cadavers tend to be consumed (at least partly) in situ, which allows cadaveric material to enter the soil (Coe 1978; Towne 2000) or to be left on the soil surface as recalcitrant residues such as hair, nails or desiccated skin (Putman 1983). Thus, significant amounts of cadaveric material might only enter the soil when insects and microbes dominate cadaver decomposition or when a

cadaver is too large to be carried away in its entirety by a scavenger.

Decomposition stages and gravesoil ecology

The resource-driven selection of the decomposer community (e.g. Beijerinck 1913; Sinsabaugh et al. 2002) was repeatedly observed as the aboveground insect succession associated with cadaver decomposition on the soil surface (Holdaway 1930; Bornemissza 1957; Anderson and VanLaerhoven 1996; Richards and Goff 1997; Kocárek 2003) or the succession of marine trophic groups associated with whale falls on the floor of deep-sea ecosystems (Bennett et al. 1994; Smith et al. 1998; Baco and Smith 2003; Smith and Baco 2003). Several cadaver decomposition studies (Payne 1965; Payne et al. 1968; Micozzi 1986; Hewadikaram and Goff 1991; Anderson and VanLaerhoven 1996; Kocárek 2003; Melis et al. 2004; Carter 2005) showed that cadaver breakdown follows a sigmoidal pattern (Fig. 1). This decomposition pattern differs from the breakdown of plant and faecal matter, which are better described by an exponential decay curve (Putman 1983; Coleman et al. 2004). The discrepancy between the pattern of cadaver and plant/faecal decomposition is probably due to the complexity of the substrate and presence of skin, which will retain cadaveric moisture, and the rate at which fly larvae assimilate cadaveric material, which can also follow a sigmoidal pattern (Putman 1977). Although the rate of cadaver breakdown will vary depending on the environment (Mann et al. 1990; Fiedler and Graw 2003; Dent et al. 2004),

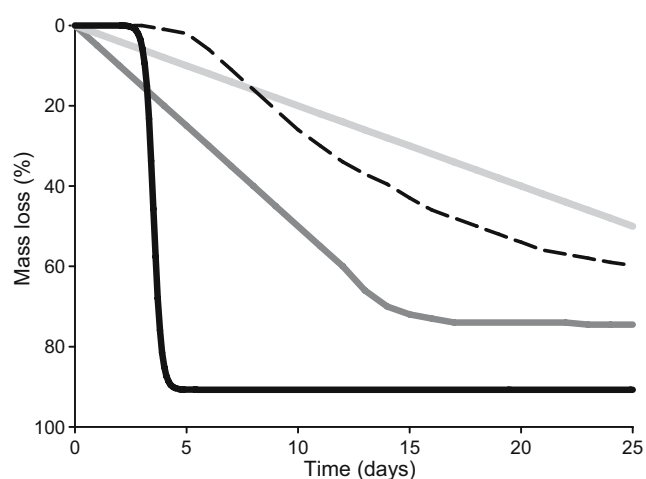


Fig. 1 Mass loss curves typically associated with the decomposition of a cadaver on the soil surface (—), buried cadaver (---), plant material (—) or faecal (dung) material (---). Cadaver mass loss data was compiled from previous publications: cadaver on soil surface (Payne 1965); buried cadaver (Carter 2005); plant material (Wardle et al. 1994; Coleman et al. 2004); faecal matter (Putman 1983; Esse et al. 2001)

it was suggested that cadavers might not persist in terrestrial ecosystems as long as faecal matter and woody material (Schoenly and Reid 1987).

The progress of a cadaver through the sigmoidal decomposition pattern is often associated with a number of stages (Fuller 1934; Bornemissza 1957; Reed 1958; Payne 1965; Payne and King 1968; Johnson 1975; Coe 1978; Megyesi et al. 2005). Decomposition stages are a convenient means to summarise physicochemical changes, however, they are subjective and do not typically represent discrete seres (Schoenly and Reid 1987). For consistency we refer to the six stages (Fresh, Bloated, Active Decay, Advanced Decay, Dry, Remains) proposed by Payne (1965). It is important to note that the progress of a cadaver through these stages is typically attributed to temperature. Accumulated degree days (ADDs: the sum of average daily temperature) can be used to compensate for differences in temperature (Vass et al. 1992; Megyesi et al. 2005). Consequently, it is known that ‘Advanced Decay’ and ‘Remains’ associated with a 68 kg human cadaver occur at 400 and 1,285 ADDs, respectively (Vass et al. 1992). Thus, an average summer daily temperature of 25°C would result in the onset of ‘Advanced Decay’ after 16 days while an average daily winter temperature of 5°C would result in an onset of ‘Advanced Decay’ after 80 days.

‘Fresh’ stage decomposition is associated with the cessation of the heart and the depletion of internal oxygen. A lack of oxygen inhibits aerobic metabolism, which causes the destruction of cells by enzymatic digestion (autolysis) (Evans 1963b; Coe 1973; Gill-King 1997). Concomitantly, blow flies (Calliphoridae) and flesh flies (Sarcophagidae) colonise a cadaver to find a suitable site for the development of their offspring. Autolysis (Vass et al. 2002) and fly colonisation (Payne 1965; Nuorteva 1977) can begin within minutes of death. Fly oviposition is a vital step in the breakdown of a cadaver as maggot activity is the driving force behind the removal of soft tissue in the absence of scavengers. Indeed, Linnaeus (1767) stated that “three flies could consume a horse cadaver as rapidly as a lion”. In addition, soil microbes (possibly zymogenous r-strategist bacteria) were observed to positively respond, as measured by carbon dioxide (CO₂-C) evolution (a commonly used index of microbial activity (Ajwa and Tabatabai 1994; Michelsen et al. 2004; Carter and Tibbett 2006)), to cadaver introduction within 24 h (Putman 1978b; Carter 2005).

The depletion of internal oxygen also creates an ideal environment for anaerobic microorganisms (e.g. *Clostridium*, *Bacteroides*) originating from the gastrointestinal tract and respiratory system. After the establishment of anaerobiosis, these microorganisms transform carbohydrates, lipids and proteins into organic acids (e.g. propionic acid, lactic acid) and gases (e.g. methane, hydrogen sulphide,

ammonia) that result in colour change, odour and bloating of the cadaver (Clark et al. 1997). This process is putrefaction and leads to the onset of the ‘Bloated’ stage (Fig. 2a).

During the ‘Bloated’ stage, internal pressure from gas accumulation forces purge fluids to escape from cadaveric orifices (mouth, nose, anus) and flow into the soil. The effect of purge fluid on belowground ecology is unknown. It is likely that this amendment results in a localised flush of microbial biomass, shift in soil faunal communities, C mineralisation (CO_2 –C evolution) and increase in soil nutrient status. This effect would be similar to the formation of discrete ‘islands of fertility’ observed in association with plant (Zaady et al. 1996) and faecal (Willott et al. 2000) resources. Eventually, putrefactive bloating and maggot feeding activity cause ruptures in the skin. These allow oxygen back into the cadaver and expose more surface area for the development of fly larvae and aerobic microbial activity (Putman 1978b) (Fig. 2b). This designates the beginning of ‘Active Decay’ (Johnson 1975; Micozzi 1986).

‘Active Decay’ is characterised by rapid mass loss (Fig. 1) resulting from peak maggot activity and the beginning of a substantial release of cadaveric fluids into the soil via skin ruptures and natural orifices (Fig. 2b). This flux of cadaveric material into the soil will connect any islands of fertility

resulting from purge fluid and, thus, lead to the formation of a single cadaver decomposition island (CDI). The status of soil nutrients and microbial communities during ‘Active Decay’ is unknown. However, Bornemissza (1957) observed an increase in some members of soil faunal community (Calliphoridae, Histeridae, Ptiliidae, Staphylinidae) and a decrease in numbers of Collembola and Acari beneath a guinea pig (*Cavia porcellus* L.) cadaver (~620 g) during ‘Active Decay’, although this decomposition stage was referred to as “Black Putrefaction”. ‘Active Decay’ will continue until maggots have migrated from the cadaver to pupate. This phenomenon represents the onset of ‘Advanced Decay’.

The lateral extent of a CDI during ‘Advanced Decay’ is determined by the size of the cadaver, the lateral extent of the maggot mass (including the path of maggot migration: Fig. 2c) and soil texture. Soil texture and cadaver size also affect the vertical extent of a CDI. For example, during ‘Advanced Decay’, Coe (1978) observed the CDI in sandy loam soil associated with elephant (*Loxodonta africana* Blumenbach) (~1,629 kg) decomposition extending to 40 cm below the cadaver, 35 cm at 1 m from the cadaver, and 8 cm at 2 m from the cadaver. No penetration into the soil was observed at 2.2 m from the cadaver. In contrast, the CDI associated with the decomposition of a 633 kg elephant cadaver on quartz gravel extended to 1.5 m below

Fig. 2 Decomposition of a 10 week old (~40 kg) pig (*Sus scrofa* L.) cadaver during the summer of 2005 at the University of Nebraska-Lincoln Agricultural Research and Development Center near Ithaca, NE, USA. **(a)** Depicts the ‘Bloated’ stage approximately 48 h after death. The onset of ‘Active Decay’ **(b)** can be designated by skin ruptures that result in the loss of moisture and increased surface area for maggot development. The release of cadaveric fluids and/or maggot activity results in the formation of a cadaver decomposition island (CDI) that is visible as dead plant material **(c)**: bar represents 1 m). The arrow denotes the path and direction of maggot migration. Approximately 80 days after death the cadaver decomposition island (CDI) is surrounded by an area of increased plant growth **(d)**, which might be used as a marker for the onset of the ‘Dry’ stage of decomposition



the soil surface (Coe 1978). By comparison, the CDI associated with the decomposition of a 620 g guinea pig (*Cavia porcellus* L.) extended to 14 cm below the cadaver in sandy soil (Bornemissza 1957).

A CDI during ‘Advanced Decay’ represents an area of increased soil carbon (Putman 1978b; Vass et al. 1992; Carter 2005), nutrients (Vass et al. 1992; Towne 2000; Carter 2005) and pH (Vass et al. 1992; Carter 2005). These changes are not surprising when we take into account that a cadaver contains a large amount of water (50% to 80%) and has a narrow C:N ratio (Tortora and Grabowski 2000; DeSutter and Ham 2005) (Table 1). These properties are characteristic of a high quality resource that is associated with a significant amount of available C, high level of microbial activity and rapid rate of nutrient input (Swift et al. 1979). These characteristics become magnified upon consideration that, for example, a fresh elephant (*Loxodonta africana* Blumenbach) cadaver can weigh 1,629 kg (Coe 1978) while a heap of elephant dung might weigh 4.5 kg (Anderson and Coe 1974).

Putman (1976, 1978b) observed that approximately 1 mg CO₂-C per gram (g⁻¹) cadaver (dry weight) was

evolved from gravesoil associated with rat (*Rattus rattus* L.) cadavers. If we assume that the soil microbial biomass assimilates 20–40% of available C (Smith 1982) then a total of 1.25–2.5 mg C g⁻¹ cadaver (dry weight) was introduced to the soil during the course of decomposition. After maggot migration, this input was associated with an increase of 1.4–2.7 μg CO₂-C g⁻¹ cadaver (dry weight) per hour (h⁻¹) during cold seasons and 41–68 μg CO₂-C g⁻¹ cadaver (dry weight) h⁻¹ during warm seasons (Putman 1976, 1978b). By comparison to other organic resources, Putman (1983) demonstrated that similar levels of CO₂-C can evolve during the decomposition of faecal matter (millipede pellets: *Glomeris marginata* Villers, 1789) (Nicholson et al. 1966) and plant litter (redbud leaves: *Cercis canadensis* L.) (Witkamp 1966). However, peak levels of microbial activity associated with faecal and plant resources tend to occur immediately after introduction to the soil when the readily available components are accessible. This is in contrast to cadaver decomposition where the majority of readily available energy and nutrients enter the soil after maggot migration (Advanced Decay) (Vass et al. 1992).

Table 1 Chemical composition of cadaveric, plant and faecal resources

| Organic resource | H ₂ O (%) | C:N ratio | N (g kg ⁻¹) | P (g kg ⁻¹) | K (g kg ⁻¹) | Ca (g kg ⁻¹) | Mg (g kg ⁻¹) | References |
|--|----------------------|-----------|-------------------------|-------------------------|-------------------------|--------------------------|--------------------------|--|
| <i>Cadaver</i> | | | | | | | | |
| Human age: adult (total mass) | 50–75 | 5.8 | 32 | 10 | 4.0 | – | 1.0 | Tortora and Grabowski (2000) |
| Human age: neonate | 69 | – | 19 | 5.6 | 2.1 | 10 | 2.6 | Widdowson (1950) |
| Pig (<i>Sus scrofa</i> L.) age: 56 days | 80 | 7.7 | 26 | 6.5 | 2.9 | 10 | 0.4 | Spray and Widdowson (1950); DeSutter and Ham (2005) |
| Rabbit (species unknown) age: 70 days | 78 | – | 29 | 7.0 | 3.2 | 12 | – | Spray and Widdowson (1950) |
| Rat (<i>Rattus rattus</i> L.) age: 70 days | 75 | – | 32 | 6.5 | 3.5 | 12 | 0.5 | Spray and Widdowson (1950) |
| <i>Plant material</i> | | | | | | | | |
| Barley straw (<i>Hordeum vulgare</i> L. cv. Welam) | – | 94 | 4.5 | – | 13.2 | – | – | Christensen (1985) |
| Wheat Straw (<i>Triticum aestivum</i> L. cv. Solid) | – | 61 | 7.0 | – | 3.9 | – | – | Christensen (1985) |
| Tobacco stem (<i>Nicotiana tabacum</i> L.) | 17 | 106 | 4.3 | – | – | – | – | Hopkins et al. (2001) |
| Beech litter (<i>Fagus sylvatica</i> L.) | 10 | – | 12 | 1.2 | 5.0 | 17.3 | 2.1 | Vesterdal (1999) |
| Norway spruce litter (<i>Picea abies</i> L. Karst) | 7.1 | – | 11 | 0.9 | 2.2 | 16.6 | 1.0 | Vesterdal (1999) |
| <i>Faecal matter</i> | | | | | | | | |
| Pig manure | – | 16 | 31 | 22 | 11 | 26 | 10 | Bernal and Kirchmann (1992) |
| Poultry manure | – | 25 | 14 | 10 | 11 | – | – | Kaur et al. (2005) |
| Dairy manure | – | 16 | 29 | 14.5 | 14.5 | 14.7 | 5.3 | Gagnon (2004) |
| Cattle manure+urine | – | 16 | 25 | 2.0 | – | – | – | Brouwer and Powell (1998) |
| Cattle manure | 82 | 22.2 | 3.8 | – | – | – | – | Calderón et al. (2005) |
| Cow manure | 84 | 18.2 | 3.9 | – | – | – | – | Calderón et al. (2005) |
| Dairy manure | 85 | 16.2 | 4.7 | – | – | – | – | Calderón et al. (2005) |

‘Advanced Decay’ is also associated with a significant increase in the concentration of soil nitrogen. The decomposition of a 68 kg human cadaver resulted in an increase in approximately $525 \mu\text{g}$ ammonium g^{-1} soil (Vass et al. 1992) by 20 days postmortem. In contrast, the amendment of 10 g soil with 200 mg fresh pig manure can result in an increase of approximately $110 \mu\text{g}$ inorganic N (ammonium, nitrate) g^{-1} soil after 63 days (Bernal and Kirchmann 1992) while the introduction of 0.6 g fresh oat (*Avena sativa* L.) roots to 150 g soil (dry weight) resulted in an increase of approximately $22 \mu\text{g}$ inorganic N g^{-1} soil over a period of 112 days (Malpassi et al. 2000). It is important to note that the introduction of any organic resource with a C:N ratio of greater than 30:1 (e.g. cereal residues, straw, woody material) (see Table 1) will usually result in an initial decrease in the concentration of soil inorganic nitrogen due to immobilisation (uptake of inorganic N by soil microbes) (e.g. Green et al. 1995). Thus, the C:N ratio will narrow during decomposition and inorganic N will be released into the soil upon reaching approximately 20:1 (see Swift et al. 1979; Stevenson and Cole 1999). However, C quality can influence this process such that a high percentage of oxidisable C can lead to immobilisation and low oxidisable C can result in mineralisation (see Smith and Tibbett 2004).

Cadaveric, plant and faecal material contains several other nutrients, such as P, potassium (K), calcium (Ca) and magnesium (Mg) (Table 1), which will enter the soil upon decomposition. Soil (3–5 cm) beneath a 68 kg human cadaver in ‘Advanced Decay’ contained $300 \mu\text{g}$ K g^{-1} soil, $50 \mu\text{g}$ Ca g^{-1} soil and $\sim 10 \mu\text{g}$ Mg g^{-1} soil (Vass et al. 1992). By comparison, the amendment of 100 g soil with fresh dairy manure at a rate of 200 mg N kg^{-1} (see Table 1) resulted in an increase of $14 \mu\text{g}$ P g^{-1} soil and $108 \mu\text{g}$ K g^{-1} soil, $159 \mu\text{g}$ Ca g^{-1} soil and $81 \mu\text{g}$ Mg g^{-1} soil after 91 days (Gagnon 2004). As much as 8 tonnes of leaf litter per hectare per year can be introduced to the soil surface of a tropical rainforest. Annual inputs per gram of litter can equate to approximately 14 mg N, 0.5 mg P, 2 mg K, 8 mg Ca, and 2 mg Mg (Ewel 1976; Scott et al. 1992). These nutrient additions, estimated to have occurred over a period of approximately 110 years, were associated with $81 \mu\text{g}$ N g^{-1} soil, $900 \mu\text{g}$ P g^{-1} soil, $8 \mu\text{g}$ K g^{-1} soil, $2,400 \mu\text{g}$ Ca g^{-1} soil and $365 \mu\text{g}$ Mg g^{-1} soil (Scott et al. 1992). While the effect of cadaver decomposition on soil nutrient status can be similar to, or less than, that observed with plant and faecal breakdown, peak nutrient values associated with cadaver decomposition can occur in much less time than required by faecal or plant materials.

While an intense pulse allows for a rapid return of energy and nutrients to the wider ecosystem, it is not always associated with a positive effect on soil biology. Decreased abundance of Collembola (0–14 cm) and Acari (0–14 cm) were observed beneath a guinea pig (*Cavia*

porcellus L.) cadaver (Bornemissza 1957). ‘Advanced Decay’ is also typically associated with the death of underlying and nearby vegetation. The cause of plant death might be due to nitrogen toxicity, smothering by the cadaver, excretion of antibiotics by fly larvae (e.g. Thomas et al. 1999) and/or some unknown factor. The intense pulse of N associated with cadaver decomposition might also result in a loss of N from the ecosystem through denitrification, volatilisation and leaching.

The transition from ‘Advanced Decay’ to ‘Dry’ to ‘Remains’ is difficult to identify (Payne 1965). Increased plant growth around the edge of the CDI (Fig. 2d) (Bornemissza 1957) might act as an indicator of the ‘Dry’ stage while increased plant growth within a CDI might indicate the ‘Remains’ stage. These final stages of cadaver decomposition correspond to a second period of slow cadaver mass loss (Fig. 1), which is probably due to the depletion of readily available nutrients and moisture. This does not mean, however, that concentration of nutrients in gravesoil have returned to basal levels. The concentration of phosphorus (Towne 2000), ammonium, potassium, sulphate, calcium, chloride and sodium (Vass et al. 1992) in soil (3–5 cm) associated with the decomposition of a 68 kg human cadaver can remain as high as $50\text{--}150 \mu\text{g}$ g^{-1} soil above basal levels during ‘Dry’ and ‘Remains’. Towne (2000) observed a concentration of inorganic N approximately $600 \mu\text{g}$ g^{-1} soil (0–10 cm) above basal levels after 1 year of bison (*Bos bison* L.) decomposition. The effect of cadaver size on C and N status becomes clearer upon the observation that soils in the center (0–5 cm) of an elephant (*Loxodonta africana* Blumenbach) CDI were observed to comprise 0.76% N and 3.25% C after 1 year of decomposition whereas control soils contained 0.05%–0.13% N and 0.20%–0.52% C (Coe 1978).

The latter stages of cadaver decomposition were also associated with a decreased abundance of Collembola (0–2 cm) and Acari (0–5 cm) (Bornemissza 1957). Conversely, ‘Dry’ and ‘Remains’ can be associated with the formation of fruiting structures of the postputrefaction fungi (Sagara 1995). It is believed that this chemoeological group of fungi fruit in response to the form and concentration of N (Tibbett and Carter 2003). ‘Early Phase’ fungi comprise zygomycetes, deuteromycetes and ascomycetes that fruit in response to high concentrations of ammonia (Yamanaka 1995a,b) from 1 to 10 months after N addition (Sagara 1992). ‘Late Phase’ postputrefaction fungi fruit in response to organic N and high concentrations of ammonium and nitrate (Yamanaka 1995a,b) and are present from 1 to 4 years after N addition (Sagara 1992). These findings, along with the observation that bison (*Bos bison* L.) (Towne 2000) and muskox (*Ovibos moschatus* Zimmerman) (Danell et al. 2002) decomposition can affect the structure of plant communities for at least 5

and 10 years, respectively, show that a CDI is a long-lasting component of terrestrial ecosystems. This is similar to the effect of organic and sulphide enrichment of sediments associated with whale falls in deep-sea marine ecosystems (Smith et al. 1998).

Cadaver burial and gravesoil ecology

Although the majority of cadavers that die in nature are located on the soil surface, a number of studies were conducted to understand cadaver decomposition after burial in soil (Motter 1898; Mant 1950; Lundt 1964; Payne et al. 1968; Sagara 1976; Lötterle et al. 1982; Rodriguez and Bass 1985; DeGaetano et al. 1992; Child 1995; Spennemann and Franke 1995; VanLaerhoven and Anderson 1999; Hopkins et al. 2000; Fiedler et al. 2004; Carter 2005; Forbes et al. 2005a, 2005a–c; Weitzel 2005; Carter and Tibbett 2006). While the results from these studies might be of little interest to the terrestrial ecologist, this aspect of belowground ecology merits attention because it might be of significance to the archaeologist, forensic scientist, and those concerned with animal composting or the disposal of farm animals.

The burial of a cadaver in soil restricts the access of most insects and scavengers. The absence of these organisms results in significantly less cadaver decomposition than observed on the soil surface (Rodriguez and Bass 1985; Rodriguez 1997; VanLaerhoven and Anderson 1999; Fiedler and Graw 2003). It is generally accepted that coarse-textured (sandy) soil with a low moisture content frequently promotes desiccation (Mant 1950; Santarsiero et al. 2000; Fiedler and Graw 2003). This phenomenon is almost certainly related to the diffusion of gases through the soil matrix (see Tibbett et al. 2004). Coarse-textured soils are associated with a high rate of gas diffusivity (Moldrup et al. 1997), which allows gases and moisture to move relatively rapidly through the soil matrix. The ability of coarse-textured soil to rapidly lose moisture will also promote desiccation because hydrolytic enzymes associated with the cycling of carbon and nutrients are retarded by low moisture content (Skujins and McLaren 1967). Desiccation can inhibit decomposition and result in the natural preservation of a cadaver for thousands of years (Micozzi 1991). However, this phenomenon only occurs in a few extreme settings such as areas of Egypt (Ruffer 1921; Dzierzykray-Rogalsky 1986), Peru (Allison 1979) and Siberia (Lundin 1978). Alternatively, burial in coarse-textured soil with a high water content might result in the formation of pseudomorphs (shapes of human cadavers primarily in the form of sand), such as those observed at Sutton Hoo, England (Bethell and Carver 1987). These pseudomorphs are associated with an elevated concentra-

tion of calcium, phosphorus and manganese, which is likely related to the breakdown of bone.

Fine-textured (clayey) soil was associated with an inhibition of cadaver breakdown (Turner and Wiltshire 1999; Hopkins et al. 2000; Santarsiero et al. 2000). These soils are associated with a low rate of gas diffusivity. The burial of a cadaver in a wet, fine-textured soil can result in decreased decomposition (Turner and Wiltshire 1999; Hopkins et al. 2000) because the rate at which oxygen is exchanged with CO₂ might not be sufficient to meet aerobic microbial demand (Carter 2005). Thus, reducing conditions are established whereby anaerobic microorganisms dominate decomposition. These organisms are less efficient decomposers than aerobes (Swift et al. 1979).

Reducing conditions can also promote the formation of adipocere (Fiedler and Graw 2003; see Forbes et al. 2004, 2005b) around a cadaver and/or internal organs, which significantly slows cadaver decomposition (Froentjes 1965; Dent et al. 2004; Fiedler et al. 2004). Many mammals (human, pig, sheep, cow, rabbit) contain sufficient moisture and fat to form adipocere in a moist coarse-textured soil (Forbes et al. 2005a,b). Gravesoil associated with adipocere formation was observed to contain elevated levels of dissolved organic C, plant available P and total P (Fiedler et al. 2004) relative to soils without adipocere. While acidic soil can promote the leaching of P from bone (Eidt 1977), significant amounts can also be released from soil saturated with P (such as gravesoils) under reducing conditions (Scalenghe et al. 2002). This release is enhanced by the presence of organic carbon, which acts as the primary electron donor (Scalenghe et al. 2002).

Few estimates of soil microbial biomass associated with reducing conditions were reported (Hopkins et al. 2000; Fiedler et al. 2004). Fiedler et al. (2004) observed a decrease in soil microbial biomass carbon estimated using the chloroform-fumigation extraction (CFE) method (Vance et al. 1987; Wu et al. 1990). Hopkins et al. (2000) observed an increase in soil microbial biomass carbon estimated using the substrate-induced respiration (SIR) method (Anderson and Domsch 1978; Hopkins and Ferguson 1994). The reason for this discrepancy is unknown, although a difference in depth of burial was suggested (Fiedler et al. 2004). While it is possible that soil depth might explain this difference it is critical to recognise that each of these methods estimates different fractions of the soil microbial biomass. SIR estimates the biomass of glucose-responsive microbes whereas CFE estimates the extracted carbon associated with fumigation of soil. Thus, it is possible to have a decrease in the whole soil microbial biomass coincide with an increase in glucose-responsive biomass (see Dilly and Munch 1998). It is also important to note that the formation of adipocere is not necessarily an endpoint (Evans 1963a; Froentjes 1965). Upon transloca-

tion to the soil surface or the establishment of an aerobic environment, adipocere can undergo decomposition (Evans 1963b). This process is typically associated with the bacteria *Bacillus* spp., *Cellulomonas* spp. and *Nocardia* spp. (Pfeiffer et al. 1998).

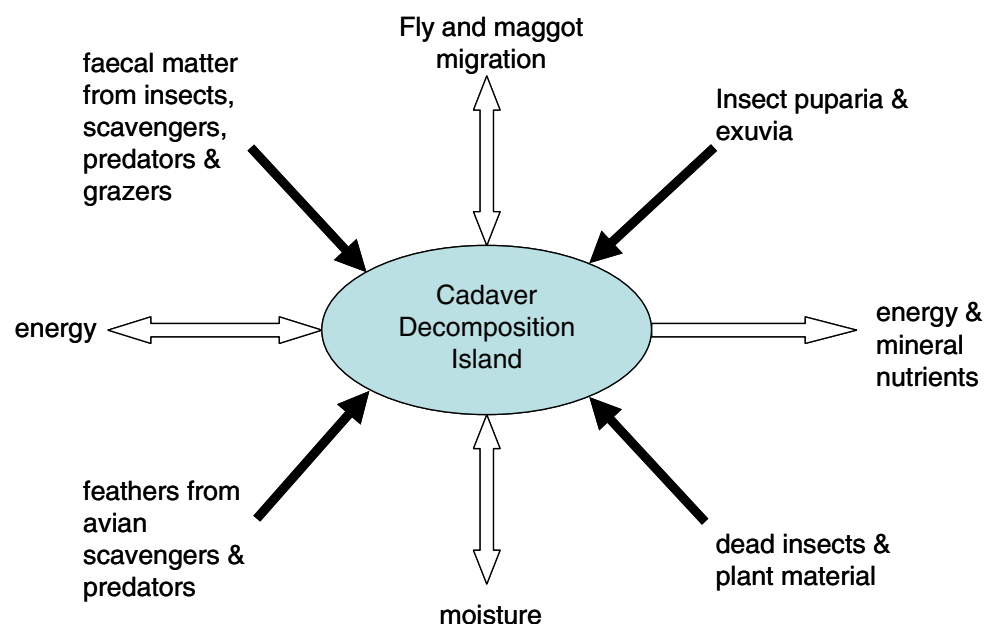
The role of cadaver decomposition in terrestrial ecosystems

Cadaver decomposition (and the formation of a CDI) is a natural disturbance that can dramatically alter steady-state edaphic and biological characteristics (Hopkins et al. 2000; Towne 2000). This represents a striking example of the linkage between aboveground and belowground communities whereby the death of aboveground organisms exert positive and negative effects on belowground organisms (e.g. Gehring et al. 2002; Wardle 2002; Wardle et al. 2004). This linkage almost certainly represents a vital pathway of carbon and nutrients in terrestrial ecosystems (as proposed by Swift et al. (1979), Odum (1959) and Coe (1978)) considering that a substantial number of animals can die from causes other than predation (Coe 1978; Young 1994) leaving their cadavers to decompose and nutrients to be recycled. Although live mammals enrich soils with materials such as faeces, hair and antlers, the carbon and nutrients immobilised by a mammal are unavailable to the wider ecosystem until death and decomposition occur (Putman 1983). Because of this, living mammals can be viewed as bottlenecks in the cycling of carbon, nutrients and water (Putman 1983).

Every CDI is a discrete, ephemeral ‘hot spot’ (Parkin 1987; Coleman et al. 2004) of activity, analogous to a rhizosphere and drilosphere, because it represents a small proportion of terrestrial area but accounts for a significant amount of heterotrophic activity within an ecosystem. Much of this activity is directed towards the cycling of cadaveric materials out to the wider ecosystem. However, a CDI also receives additional organic and inorganic materials resulting from the activity of scavengers, grazers and predators. During early stages of cadaver breakdown these inputs might include faecal matter and/or components (hair, nails, feathers) from scavengers. During later stages of decomposition, the soil can be amended with faecal matter from grazers attracted to the enhanced plant growth surrounding a CDI (Towne 2000) or from predators that hunt these grazers (Gray 1993). Insect and avian materials might represent a significant influx of chitin and keratin, respectively. Thus, a CDI acts as a highly concentrated hub of carbon and nutrient flow (Fig. 3) that can be scattered across a landscape and, therefore, contribute to landscape complexity and heterogeneity.

The importance of the heterogeneous distribution of cadaveric material in soil cannot be understated as it can facilitate niche provision and hence biodiversity in an ecosystem. A CDI contributes directly to biodiversity by acting as a specialised habitat for the reproduction of the majority of blow flies (Calliphoridae) (Hall 1948), Dermestid (Dermestidae) beetles, carrion beetles (Silphidae) and burying beetles (Silphidae) (Meierhofer et al. 1999; Smith and Merrick 2001). The presence and activity of these insects may affect other trophic levels (bacteria, fungi,

Fig. 3 Diagram of the cadaver decomposition island (CDI) as a highly concentrated hub of energy and nutrient flow that contributes to landscape heterogeneity, physical and chemical complexity and biodiversity in a terrestrial ecosystem



protozoa, nematodes). For example, insects can establish phoretic relationships with a number of nematodes (Poinar 1983; Richter 1993). Furthermore, a CDI supports the establishment of pioneer plant species because the pulse of nutrients and death of vegetation associated with cadaver decomposition is a disturbance of high resource quality and reduced competition (Towne 2000). A change in plant community structure will, in turn, probably affect soil microbial communities (Johnson et al. 2003) and the organisms that feed upon them (e.g. nematodes, protozoa). This cascade effect, as Towne (2000) pointed out, is part of a cycle of disturbance and recovery that has enriched ecosystems for eons.

Cadaveric material has a significant impact on below-ground ecology when circumstances allow for in situ decomposition. The breakdown of cadavers and cadaver components (e.g. skeletal muscle tissue, bone) is associated with an increase in soil microbial biomass (Child 1995; Hopkins et al. 2000; Carter and Tibbett 2006), soil microbial activity (Putman 1978b; Hopkins et al. 2000; Carter and Tibbett 2006) and nematode abundance (Todd et al. 2006). Cadaveric breakdown also results in an increase in the concentration of ammonium (Vass et al. 1992; Hopkins et al. 2000; Towne 2000; Carter 2005), phosphorus (Bethell and Carver 1987; Towne 2000), calcium, potassium, sulphate, magnesium, chloride, sodium (Vass et al. 1992) sulphur (Hopkins et al. 2000), manganese (Bethell and Carver 1987) and base cations (Rodriguez and Bass 1985; Vass et al. 1992; Hopkins et al. 2000; Carter 2005).

Clearly, our knowledge of the belowground ecology of cadaver decomposition is limited. This is in direct contrast with the decomposition of other organic resources such as plant leaves (Webster et al. 2000), stems (Hopkins et al. 2001), root exudates (Dakora and Phillips 2005), seeds (Tibbett and Sanders 2002) and sewage sludge (Ajwa and Tabatabai 1994). This discrepancy is probably because forensic taphonomy has primarily relied upon case studies, anecdotal evidence and unreplicated experiments for data (Mant 1950; Morovic-Budak 1965; Sagara 1976; Rodriguez and Bass 1985; Micozzi 1986; Galloway et al. 1989; Mann et al. 1990; Prieto et al. 2004). Techniques commonplace in ecological research should be applied to the materials relevant to forensic taphonomy (cadavers, cadaver components). A long-term goal of this research should be to more accurately account for the contribution of cadaver decomposition to the cycling of carbon and nutrients in terrestrial ecosystems. Since the majority of decomposition in soil is microbially mediated (Moorhead and Reynolds 1989) future investigations might focus on belowground community assemblages and succession. Several techniques are currently used for studying soil microbial communities (Kirk et al. 2004). These can provide a profile of the whole soil community (such as via fatty acid methyl esters

(Drijber et al. 2000) or phospholipid fatty acid methyl esters (Pankhurst et al. 2001; Carter 2005), bacterial community (Horswell et al. 2002), or individual species (Rhodes et al. 1998). A molecular approach to the study of microbial diversity has proven helpful in the investigation of sediments associated with whale falls (Tringe et al. 2005).

A fundamental understanding of gravesoil ecology should, in turn, contribute to forensic taphonomy by designating biological and chemical markers with the potential to aid in the location or dating of clandestine graves such as the fruiting sequence of postputrefaction fungi (Carter and Tibbett 2003) or the nutrient concentration of gravesoils (Vass et al. 1992). Forensic science could benefit from the development of a method to estimate postmortem interval after 1,285 ADDs, when the concentration of volatile fatty acids (propionic, valeric, butyric) returns to basal levels (Vass et al. 1992). This work would likely require investigating the postputrefaction fungi, ratios of the longer chained FAMES, or possibly examining the community dynamics of microfungi (e.g. Lumley et al. 2001). Some strains of microfungi are capable of breaking down keratin, which is the primary component of hair and nails. As such, this component is likely to represent a significant portion of available carbon and nutrients during 'Remains' stage decomposition. Whatever research paths are taken, it is clear that gravesoil ecology and the ecology of other ephemeral resource patches (Blaustein and Schwartz 2001; Finn 2001; De Meester et al. 2005) has the potential to become a key area of study in terms of the cycling of carbon and nutrients, soil organic matter formation and the relationship between biodiversity and ecosystem function.

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