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REWRITING ECOLOGICAL SUCCESSION HISTORY: DID CARRION ECOLOGISTS GET THERE FIRST?

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ABSTRACT
Ecological succession is arguably the most enduring contribution of plant ecologists and its origins have never been contested. However, we show that French entomologist Pierre Mégnin, while collaborating with medical examiners in the late 1800s, advanced the first formal definition and testable mechanism of ecological succession. This discovery gave birth to the twin disciplines of carrion ecology and forensic entomology. As a novel case of multiple independent discovery, we chronicle how the disciplines of plant and carrion ecology (including forensic entomology) accumulated strikingly similar parallel histories and contributions. In the 1900s, the two groups diverged in methodology and purpose, with carrion ecologists and forensic entomologists focusing mostly on case reports and observational studies instead of hypothesis testing. Momentum is currently growing, however, to develop the ecological framework of forensic entomology and advance carrion ecology theory. Research-

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ers are recognizing the potential of carcasses as subjects for testing not only succession mechanisms (without assuming space-for-time substitution), but also aggregation and coexistence models, diversity-ecosystem function relationships, and the dynamics of pulsed resources. By comparing the contributions of plant and carrion ecologists, we hope to stimulate future crossover research that leads to a general theory of ecological succession.

INTRODUCTION

MULTIPLE independent discovery (Lamb and Easton 1984) has occurred sporadically in science throughout its recent history. Some of these discoveries were simultaneous or almost so, while others occurred in mutual isolation, sometimes many years apart (Merton 1961). In the ecological sciences, examples include (but are not limited to) the theory of evolution by natural selection (Darwin 1858, 1859; Wallace 1859), the equilibrium theory of island biogeography (Munro 1948; MacArthur and Wilson 1963; Brown and Lomolino 1989), and allometric scaling of population variance with mean body size (Marquet et al. 2005; Cohen et al. 2012). Ecological succession, the change in species composition in communities over time (as defined by Cain et al. 2008), is arguably the oldest and most enduring concept in ecology (Cherrett 1989). Modern general ecology textbooks repeatedly identify Cowles (1899), Clements (1916, 1936), and Gleason (1917, 1926, 1939)—in various combinations—as succession's earliest theorists (e.g., Stiling 2002; Cain et al. 2008; Krebs 2009; Smith and Smith 2012; Molles 2013). Hence, the origin of ecological succession theory has never been questioned. However, here we show that French veterinarian and entomologist Pierre Mégnin, while collaborating with medical examiners to document the succession of insects on exhumed and exposed human corpses (Mégnin 1883, 1887, 1894), advanced the first formal definition and testable mechanism of ecological succession. This discovery gave birth to carrion ecology and its applied cousin, forensic entomology, which uses thermal development and successional timetables of insects on corpses to estimate time since death of the deceased in criminal investigations (Byrd and Castner 2010).

The fields of plant and carrion ecology originated and developed independently, and given their disparity in subject matter, training, and institutional structures, we show that these two groups were unaware of each other's publications. Nevertheless, these groups accumulated strikingly similar parallel histories and contributions, which we also chronicle below. One difference is, however, obvious. Breakthroughs in plant ecology, notably the paradigm shift from the Clementsian school (Clements 1916, 1936) to the Gleasonian school (Gleason 1917, 1926, 1927, 1939) and the introduction of testable models and mechanisms (Horn 1975; Connell and Slatyer 1977; Hill et al. 2004; Solow and Smith 2006), shaped the theoretical development of succession. By contrast, carrion ecology and forensic entomology diverged from basic ecological thinking about succession due to their emphases on insect taxonomy and observational studies throughout the 20th century (Michaud et al. 2012). Mechanisms developed for plant and marine communities (Connell and Slatyer 1977) carried over to carrion succession without empirical support (Connell and Slatyer 1977; Schoenly and Reid 1987; Smith and Baco 2003) and, as a result, little is known about the mechanisms that drive succession on carrion as well as other ephemeral and patchy resources (e.g., dung, leaf litter, fallen fruits, rotting logs).

In this paper, we chronicle the independent discovery and formalization of plant and carrion-arthropod succession, and examine the paradigm shifts that redirected plant ecology and the twin disciplines of forensic entomology and carrion ecology into what they are today. Such comparisons, we hope, will stimulate future crossover research that leads to a general theory of ecological succession.

PARADIGMS OF PLANT SUCCESSION

Early documentation of plant communities by European naturalists (De Luc 1806 as cited in Rennie 1810; Dureau de la Malle 1825; Hult 1885, 1887; Warming 1891) helped mark the birth of ecology. According to Clements (1916), De Luc (1806; as cited in Rennie 1810) was the first naturalist to coin the word "succession," Hult (1885, 1887) conducted the first systematic study of vegetation development and established the concept of a climax assemblage, and Warming (1891) was the first to give a consistent account of succession on sand dunes. Early European botanists also provided the necessary observations that plant ecologists would later build upon to formalize a conceptual framework of plant succession.

One of the first naturalists to apply the term "succession" and offer a functional explanation was American naturalist Henry David Thoreau (1860). Through his own observations, Thoreau also refuted old thinking that seeds spontaneously generate or lay dormant for centuries and showed instead that they become dispersed by wind and animals. Thoreau described a particular case involving pine trees and oaks, and how every time a pine tree was cut down an oak tree sprung up, and vice versa. When pines were cut down, conditions became favorable for the oaks and the latter grew larger. After a few years, the area became unfavorable for the oaks and, in turn, pines were again allowed to grow. Thoreau called this trend "forest succession." Likewise, Darwin (1859) proposed that cleared forests eventually supported the same species as surrounding forests and, later, Douglas (1875, 1889) chronicled the fate of pioneer species in burned forests.

Despite the early accounts of Thoreau, Darwin, and Douglas, a decade passed before succession was formalized as an ecological concept in North America. Cowles (1899) described the coastal region of Lake Michigan, its various dune formations, and vegetation, including the transition from beach to mesophytic forest. Cowles also used the term "climax" to describe the last, most mature stage of vegetation within a geographic area. Subsequently, Cowles (1901) defined the mesophytic forest as a climax assemblage, but this time for inland and coastal environments. Cowles described the order of succession and how plant communities replaced each other when conditions changed, a phenomenon driven mostly by climate, and he assumed that changes in space mirrored those in time, known today as space-for-time substitution (Pickett 1989). Cowles wrote:

> The various plant societies pass in a series of successive types from their original condition to the mesophytic forest, which may be regarded as the climax or culminating type . . . stages may be slow or rapid . . . stages may be direct or tortuous (Cowles 1901: 80-81).

Thus, Cowles (1899, 1901) was the first ecologist to define succession as a sequential and directional process ending in a climax community. Tansley later wrote:

> It is to Henry Chandler Cowles that we owe, not indeed the first recognition or even the first study of succession, but certainly the first thorough working out of a strikingly complete and beautiful successional series . . . Cowles did far more than any one else to create and to increase our knowledge of succession and deduce its general laws (Tansley 1935:284).

Research by pioneering botanists such as Hult (1885, 1887), Warming (1891), and Cowles (1899, 1901) helped to usher in ecology as a distinct discipline. By the early 1900s, Frederic E. Clements (1916, 1936) had developed his monoclimax theory of succession, which became ecology's first paradigm (Simberloff 1980). The premise of Clements' work, based loosely on Cowles' ideas, was that succession behaved like an organism, developing from different unstable stages called seres, to a final stable sere called a climax, all under control of the regional climate. In his youth, Clements saw a boom-and-bust cycle of agricultural expansion play out on the Midwestern prairies by pioneer homesteaders whose poor farming and grazing practices brought drought and famine (Tobey 1981). Clements and his fellow grassland ecologists, who included his mentor Charles E. Bessey and Roscoe Pound at the University of Nebraska, championed a dynamic version of plant ecology in the early 1900s that depended on quadrats (including permanent and denuded versions), experimental and graphical methods, and quantitative approaches (Worster 1994; Kingsland 2005). Using the quadrat method, Pound and Clements ([1898] 1977) found that vegetation along the slope of the Great Plains varied more than expected, "even though to the eye there was no change" (Tobey 1981: 71). By comparing vegetation in roadways with those in right-of-way enclosures (fenced off by the railroad), Clements showed what the prairie landscape, when left undisturbed, looked like (Kingsland 2005). These perceptions and observations developed into the Clementsian school that emphasized the closed-ended, sequential, directional, and predictable nature of succession and identified facilitation as its chief mechanism (i.e., pioneer colonizers modify their environment, making it unsuitable for themselves but suitable to others). Clementsian succession, which was considered dogma in the first half of the 20th century, nevertheless offered an experimental approach for studying succession (Tobey 1981; Kingsland 2005) and stimulated a groundswell of research that still finds applications today (Pickett et al. 2009).

The second view, based on field studies of Henry Gleason (1917, 1926, 1927, 1939) and Leonty Ramensky (1924), shifted attention away from the superorganism view to one that emphasized the community's dependence on environmental gradients, life histories of individual species, stochastic events, and variable arrival times of colonizers. The individualistic concepts of Gleason and Ramensky were deeply rooted in extensive floristic studies they had conducted in their home countries of America and Russia, respectively. Like Clements, Gleason employed quadrats and they were among the earliest ecologists to use them to study the distribution and frequency of individual terrestrial plants (McIntosh 1985). In his landmark 1926 paper, Gleason concluded:

> it may be said that every species of plant is a law unto itself, the distribution of which in space depends on its individual peculiarities of migration and environmental requirements (Gleason 1926:26).

In opposition to Clements, Gleason argued for a more flexible view of succession and rejected Clements' notion of irreversibly directed seres and the monoclimax. Gleason's papers, however, had little impact on his contemporaries, and were largely ignored. Even before Gleason published his last paper on succession in 1939, he had decided to leave ecology to pursue plant taxonomy for which he had a long and distinguished career (McIntosh 1975). Although the Gleasonian view was overlooked for decades, by the 1950s the contributions of John T. Curtis (i.e., ordination) and Robert H. Whittaker (i.e., gradient analysis) had persuaded many plant ecologists that Gleason's individualistic concept was valid (Gurevitch et al. 2006). By 1949, the first American textbook on animal ecology (Allee et al. 1949) had at least cited Gleason's papers on the individualistic concept (McIntosh 1975); however, it took another decade for Gleason's succession model to carry over into animal ecology (McIntosh 1995).

Today, modern ecology textbooks continue to portray the Clementsian and Gleasonian schools as a dichotomy from which few ecologists have diverged; the few that did included Cooper (1926), Tansley (1935), Whittaker (1953), Horn (1975), and Pickett (1976). These slightly divergent approaches, however, never quite caught on. McIntosh (1975) provocatively asked to what extent the power of place, namely, the Nebraska grassland for Clements and the prairie-forest border of Illinois for Gleason, informed their views on plant succession that led them to reach different conclusions. Likewise, Ramensky worked in meadows near the Oskil River region of Voronezh Province in Russia, arrived at similar conclusions as Gleason, and was also dismissed by his peers (McIntosh 1983, 1985). Today, most plant ecologists take an intermediate position between the Clements-Gleason (Ramensky) dichotomy (Gurevitch et al. 2006) and acknowledge that the methods used to sample vegetation also affects the nature of the plant association (Barbour et al. 1987). Plant ecologists still disagree, however, on the relative importance of biotic and abiotic factors and the role of stochastic events in shaping plant community structure (Barbour et al. 1987; Gurevitch et al. 2006).

Although the 1960s saw the introduction of mathematical models for plant succession (McIntosh 1999), testable hypotheses of different successional mechanisms did not appear until Connell and Slatyer (1977). In their influential paper, Connell and Slatyer (1977) described three mechanisms and offered examples for each from the literature and experimental criteria required for hypothesis testing. Briefly, in the facilitation model, only pioneer species are able to colonize. Those species modify their environment, eventually making it more suitable for the establishment of later-succession species and less suitable for other early colonists. In time, pioneer species are eliminated. In the tolerance model, any species has the potential to colonize. Those species modify the environment, eventually making it less suitable for early colonists but the ability of later-succession species to colonize is not affected. In time, pioneer species are eliminated. In the inhibition model, any species has the potential to colonize. Those species modify the environment, eventually making it less suitable for early colonists, but also inhibiting the ability of later-succession species to colonize. According to Connell and Slatyer (1977), studies on newly exposed substrates and marine benthic environments provided evidence for facilitation, whereas studies on terrestrial plants and marine organisms provided evidence for the inhibition model. No study was found to support the tolerance model. Just as the views of Clements and Gleason stimulated much debate 50 years earlier, the mechanisms of succession proposed by Connell and Slatyer (1977) underwent rapid scrutiny and refinement (e.g., Tilman 1985; Pickett et al. 1987; Farrell 1991). These developments initiated the second paradigm shift in plant succession, which continues today (e.g., Maggi et al. 2011; Marleau et al. 2011; Prach and Walker 2011).

What Cowles and his European predecessors and colleagues did was document the first successional series, apply the word "succession," and provide a general framework of the mechanism involved. Coincidentally, a veterinarian-entomologist and his medical examiner colleagues in France were studying the same phenomenon, but in a more macabre context.

PARADIGMS OF FORENSIC ENTOMOLOGY AND CARRION ECOLOGY

Forensic (or medicolegal) entomology emerged out of the much older and larger discipline of forensic medicine whose origins date back to Egypt nearly 3,000 years ago (Smith 1951). According to Greenberg and Kunich (2002), the earliest recorded use of insects in a legal case dates back to 10th century China in which a murder investigation was recorded, set between 907 and 960 AD (Cheng 1890, cited by Greenberg and Kunich 2002). A coroner had interviewed a distraught woman who said her husband was killed by fire, but the coroner found aggregations of flies on the victim's head. At autopsy, investigators found an embedded projection in the wound. When confronted with the evidence, the woman reportedly confessed that she and an accomplice had murdered her husband (Cheng 1890). Another first for China was the publication of the earliest training manual for death scene investigators, *Hsi Yüan Chi Lu* ("The Washing Away of Wrongs"), written by Sung Tz'u in the 13th century (translated into English by Giles 1924 and McKnight in Sung 1981). Although Sung's medical knowledge was considerable, he was trained not as a physician, but as a jurist. Nevertheless, his "Instructions to Coroners" (Giles 1924) was unrivaled in detail and coverage for his day (Gwei-Djen and Needham 1988) and contained many observations, methods, tests, and collections of selected cases, including one case involving insects. A man had been found dead by the roadside with numerous head wounds that resembled those made by a sickle. After the coroner ordered 70 of the local villagers to assemble with their sickles on the ground, he noticed flies aggregating on only one, indicating that it had residual traces of blood and tissue. When confronted with the evidence, the villager reportedly confessed (Giles 1924: 77; Sung 1981:69-70). Elsewhere in the manual, Sung revealed his knowledge of fly life cycles, their appearance in decomposing bodies in different seasons of the year, and observations on their infestation in the nine natural orifices and wounds of the body (Giles 1924:68-69; Sung 1981:86–87).

In Europe, the coroner system (i.e., coroners being responsible officials of the Crown) was established in the late 12th century, whereas expert testimony in death investigations was formalized in the 13th century (Sung 1981). When English colonists came to America, they brought their coroner system with them (Hanzlick 2007). Coroners were often elected officials with no medical training. The earliest American legislation to require elected coroners to have medical training did not occur until the 1870s, which eventually led to a gradual shift toward the medical examiner system (Hanzlick and Combs 1998). Currently, 31% of the counties in the U.S. are served by medical examiners (Hanzlick 2007).

One of the earliest known documentations of the role of insects in decomposition originated in Europe and was used to refute spontaneous generation when Italian physician Francesco Redi (1668) experimentally demonstrated, using meat, small carcasses, and proper controls, that maggots come from adult flies. Redi also documented the successive emergence from the substrate of different types of adult flies. He did not use the term "species" as his work preceded Linnaeus (1767), but his descriptions matched those of Calliphoridae (two or three species), Sarcophagidae and/or Muscidae, and probably Sepsidae. However, Redi did not monitor visitation or oviposition behavior of different fly species, and as such did not allude to any successional process. From his field observations and taxonomic treatment of carrion-breeding flies, Linnaeus wrote a century later:

> Three flies consume the corpse of a horse as quickly as a lion did (Linnaeus 1767: 990).

Over the succeeding decades, European physicians, while conducting autopsies, also encountered (but largely ignored) carrion insects. Although Orfila and Lesueur (1831) suspected that insects could play a role in legal medicine, they did not include a discussion of insect succession or how insects could be used in such investigations. Bergeret (1855) used insects to solve a homicide involving a mummified infant found in an apartment's chimney in March 1850. The autopsy revealed the presence of pupae and maggots of the flesh fly *Musca carnaria* (now *Sarcophaga carnaria*; Diptera: Sarcophagidae) and a moth (named "Papillon des mites"; most likely Lepidoptera: Tineidae), an early and late colonizer, respectively. Bergeret used his limited knowledge of entomology as a tool to estimate time of death and concluded that investigators should focus their case on previous tenants of the apartment. Although Bergeret (1855) misinterpreted the life cycles of some of the insects in this case (Goff 2000; Benecke 2008), it was the first time entomology was used to estimate time of death and also the first documented case in which succession was described. The term "succession," however, was never used. Three decades later, the German physician Hermann Reinhard (1882), conducted the first taxonomic survey of the fauna of exhumed corpses, identifying seven arthropod taxa (i.e., coffin flies, braconid wasps, latrine flies, millipedes, rove beetles (two species), and graveyard beetles).

The first biologist to provide a comprehensive account of succession, to make use of the term, and to hypothesize on its underlying mechanisms was French army veterinarian and entomologist Pierre Mégnin (1883, 1887, 1894) who collaborated with Paul Brouardel, a French medical examiner (Brouardel 1879) who also worked on tuberculosis and vaccination (Benecke 2008). Mégnin, who started his collaboration with Brouardel in 1878 by identifying mites from a mummified body (Benecke 2008), recognized the predictability of carrion-arthropod succession and its forensic potential. While realizing the enormous challenge posed by time-since-death estimation, Mégnin noted:

> This problem seemed insoluble. However, Brouardel suggested to me that perhaps we could use as its solution the remnants that the numerous legions of insects, succeeding each other with remarkable regularity,

> leave behind on a cadaver (translated by J.-P. Michaud; Mégnin 1883:480).

Mégnin (1883) also described three of his cases in which his estimates of time since death were corroborated by suspect confessions. Mégnin later noted that:

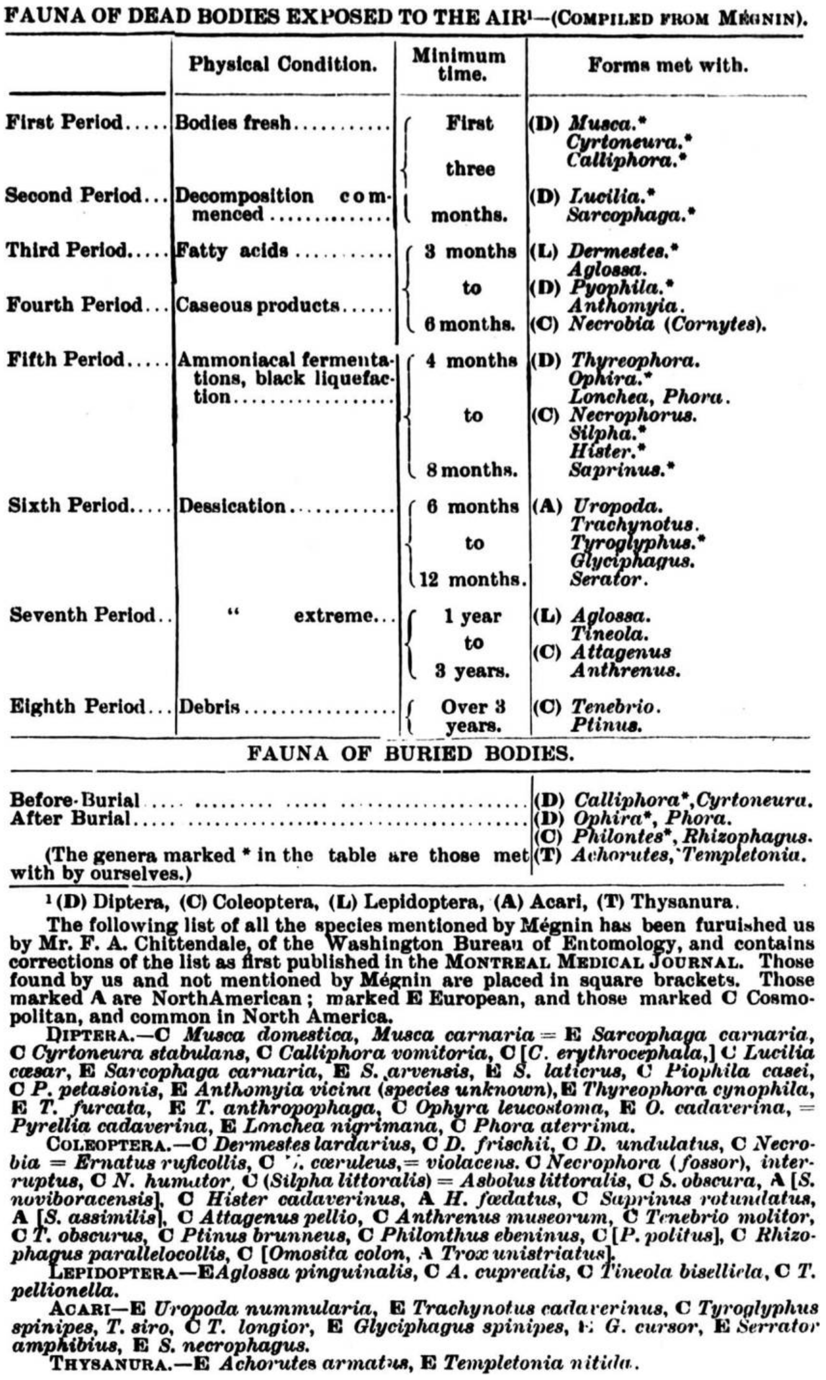
> The oviposition by insects does not occur at the same time for all; they each chose a degree of decomposition . . . that moment is so constant for each species and the succession of their apparition is so regular that we can state the age of the cadaver (translated by J.-P. Michaud; Mégnin 1887:948).

In his classic text, Mégnin (1894) summarized his case histories dating back to 1879 and expanded on his time-since-death methodology:

> For a long time a fact, which we were the first to observe, marked us: the insects that colonize cadavers, or death workers, arrive in succession and always in the same order. We counted a dozen periods between death and the complete destruction of the cadaver, and in each of those always appear the same insects . . . putrefaction occurs in a series of fermentations, and the product of each is better suited to a group of death workers than the other, which explains their regular succession (translated by J.-P. Michaud; Mégnin 1894:13).

Mégnin was referring to the action of bacteria that produced different odorous gases that became attractive to certain insects. Mégnin (1894) also described eight "squads" of arthropods (insects, mites) that succeeded each other at different times during decomposition and within each squad a distinct arthropod assemblage formed (Figure 1). In addition, Mégnin (1894) acknowledged that the arthropods in each squad could change depending on site and season. In the second half of his book, Mégnin (1894) described 19 case reports (spanning 30 years), including his own cases (some with Brouardel) between 1879 and 1890, for which he offered expert testimony. Mégnin also briefly collaborated with another French physician, G. P. Yovanovitch, of the Faculty of Medicine in Paris, who published a thesis based on Mégnin's succession tables (Yovanovitch 1888). However, without consulting Mégnin, Yovanovitch added a table at the end of his thesis that listed insect occurrences spanning five years when instead Mégnin's observations included at most 24 months. Mégnin (1889) pointed out that Yovanovitch had mistaken "periods" for "years" and asked for the table to be retracted from the thesis. Another physician inspired by Mégnin (1894) was Eduard Ritter von Niezabitowski, a medical examiner at the Medico-Legal Institute at Krakow University. Niezabitowski (1902) conducted a two-year observational study of arthropod succession using stillborn human remains and carrion from several mammal species (i.e., cat, fox, rat, mole, and calf) deployed in and around the institute's grounds and in nearby fields and forests. He collected and identified carrion-associated species belonging to several fly and beetle families and aggregated his data in a succession table that spanned 14 days of observations. Niezabitowski observed a faster rate of soft-tissue decay during summer than fall and winter, negligible preference by carrion insects for human remains over (other) animal remains, and habitat preferences of certain insects for human settlements, fields, and forests. Based on these seasonal and site differences, Niezabitowski (1902) warned that Mégnin's eight-squad classification system was neither regular nor universal in its chronology and concluded that his theory, which was based mostly on concealed remains found inside closed rooms, had limited forensic value for outdoor situations.

In North America, Wyatt Johnston and Georges Villeneuve, two Canadian physicians inspired by Mégnin, applied their observations of insect succession on corpses from several of their cases to estimate time of death (Johnston and Villeneuve 1897), but cautioned against applying Mégnin's rules to other countries and climates. The authors concurred with Mégnin (1894) as to the successional sequence and the rules governing it. American physician Murray G. Motter, working as a volunteer for the U.S. Bureau of Animal Industry (now the U.S. Agricultural Research Service), also tested the applicability of Mégnin's squads in a study of 150 exhumed corpses in the Washington, DC, area (Motter 1898). His results included detailed annotations on corpse-associated arthropods



FAUNA OF DEAD BODIES EXPOSED TO THE AIR[1]—(COMPILED FROM MÉGNIN).

	Physical Condition.	Minimum time.	Forms met with.
First Period	Bodies fresh	First three months.	(D) *Musca.** *Cyrtoneura.** *Calliphora.**
Second Period	Decomposition commenced		(D) *Lucilia.** *Sarcophaga.**
Third Period	Fatty acids	3 months to 6 months.	(L) *Dermestes.** *Aglossa.*
Fourth Period	Caseous products		(D) *Pyophila.** *Anthomyia.* (C) *Necrobia* (*Cornytes*).
Fifth Period	Ammoniacal fermentations, black liquefaction	4 months to 8 months.	(D) *Thyreophora.* *Ophira.** *Lonchea*, *Phora*. (C) *Necrophorus.* *Silpha.** *Hister.** *Saprinus.**
Sixth Period	Dessication	6 months to 12 months.	(A) *Uropoda.* *Trachynotus.* *Tyroglyphus.** *Glyciphagus.* *Serator.*
Seventh Period	" extreme	1 year to 3 years.	(L) *Aglossa.* *Tineola.* (C) *Attagenus* *Anthrenus.*
Eighth Period	Debris	Over 3 years.	(C) *Tenebrio.* *Ptinus.*

FAUNA OF BURIED BODIES.

Before-Burial	(D) *Calliphora**, *Cyrtoneura.*
After Burial	(D) *Ophira**, *Phora.* (C) *Philontes**, *Rhizophagus.* (T) *Achorutes*, *Templetonia.*

(The genera marked * in the table are those met with by ourselves.)

[1] (D) Diptera, (C) Coleoptera, (L) Lepidoptera, (A) Acari, (T) Thysanura.

The following list of all the species mentioned by Mégnin has been furnished us by Mr. F. A. Chittendale, of the Washington Bureau of Entomology, and contains corrections of the list as first published in the MONTREAL MEDICAL JOURNAL. Those found by us and not mentioned by Mégnin are placed in square brackets. Those marked A are NorthAmerican; marked E European, and those marked C Cosmopolitan, and common in North America.

DIPTERA.—C *Musca domestica*, *Musca carnaria* = E *Sarcophaga carnaria*, C *Cyrtoneura stabulans*, C *Calliphora vomitoria*, C [*C. erythrocephala*,] C *Lucilia cæsar*, E *Sarcophaga carnaria*, E *S. arvensis*, E *S. laticrus*, C *Piophila casei*, C *P. petasionis*, E *Anthomyia vicina* (*species unknown*), E *Thyreophora cynophila*, E *T. furcata*, E *T. anthropophaga*, C *Ophyra leucostoma*, E *O. cadaverina*, = *Pyrellia cadaverina*, E *Lonchea nigrimana*, C *Phora aterrima*.

COLEOPTERA.—C *Dermestes lardarius*, C *D. frischii*, C *D. undulatus*, C *Necrobia* = *Ernatus ruficollis*, C *N. cæruleus*, = *violacens*. C *Necrophora* (*fossor*), *interruptus*, C *N. humator*, C (*Silpha littoralis*) = *Asbolus littoralis*, C *S. obscura*, A [*S. noviboracensis*], C *Hister cadaverinus*, A *H. fœdatus*, C *Saprinus rotundatus*, A [*S. assimilis*], C *Attagenus pellio*, C *Anthrenus museorum*, C *Tenebrio molitor*, C *T. obscurus*, C *Ptinus brunneus*, C *Philonthus ebeninus*, C [*P. politus*], C *Rhizophagus parallelocollis*, C [*Omosita colon*, A *Trox unistriatus*].

LEPIDOPTERA—E *Aglossa pinguinalis*, C *A. cuprealis*, C *Tineola biselliela*, C *T. pellionella*.

ACARI—E *Uropoda nummularia*, E *Trachynotus cadaverinus*, C *Tyroglyphus spinipes*, *T. siro*, C *T. longior*, E *Glyciphagus spinipes*, E *G. cursor*, E *Serrator amphibius*, E *S. necrophagus*.

THYSANURA.—E *Achorutes armatus*, E *Templetonia nitida*.

FIGURE 1. FAUNA OF DEAD BODIES EXPOSED TO THE AIR

Mégnin's (1894) eight "squads" reflecting his view that distinct arthropod faunas succeed one another on a human corpse at different times in a deterministic order (Mégnin 1894:24–95). Mégnin's succession-based thinking preceded the parallel theories of Clements (1916) and Gleason (1917) by two decades. Figure reprinted from Johnston and Villeneuve (1897).

as well as tabulated data on the soil type, grave depth, and moisture content associated with each exhumed corpse. He challenged Mégnin's view that squads replace each other in an orderly sequence at precise moments throughout decomposition and cautioned against making generalizations.

Mégnin and his colleagues essentially reproduced what Cowles' predecessors and colleagues did: they observed and described successional seres, coined "succession," and provided a general framework of the mechanism involved. Both groups originated in Europe in the late 1800s. By the turn of the century, European scientists had introduced succession concepts to North America where high importance was assigned to seres (or squads) and to the role of climate in shaping successional outcomes.

Despite these promising beginnings, scientific progress and popularity in forensic entomology languished in the first half of the 20th century, except when a high-profile murder case that involved insects surfaced (Goff 2000; Benecke 2008). Over the same time period and for the rest of the century, carrion ecology remained mired in a descriptive era, notable for its many observational studies that exposed animal carcasses to different seasons and environments (e.g., Morley 1907; Jaques 1915; Illingworth 1926; Fuller 1934; Bornemissza 1957; Reed 1958; Payne 1965; Nabaglo 1973; Johnson 1975; McKinnerney 1978; Abell et al. 1982; Early and Goff 1986; Tantawi et al. 1996). Although these (and many other) reports provided detailed species lists, graphs, and tables of succession, and descriptions of decomposition, no mechanisms were proposed for the successional patterns observed.

One study in the 1960s by Jerry A. Payne, a graduate student at Clemson University, stands out for its originality and impact. First, Payne (1965) used cages with different mesh sizes to provide open and closed access to insects to study day-to-day changes in carcass decomposition, a comparison that previous researchers had not subjected to a tandem field test; Fuller (1934) studied insect-protected carrion in an insectary. Payne found that carcasses protected from insects mummified, keeping their integrity for months, whereas, carcasses exposed to insects lost 90% of their starting weight in just six days. This result showed that carrion decomposition, based on weight loss measurements, accelerated in the presence of insects. Second, after trying carrion of different sizes and from different vertebrate species (i.e., amphibians, mammals, and birds), Payne (1965) settled on domesticated pigs because he knew when they died and could acquire them in large numbers of uniform size and age. He also found that their relatively hairless skin and lack of feathers made insect sampling easier. Third, Payne (1965) published his study, not in an entomology journal, but in an ecology journal, which guaranteed a wider audience. Since this study, the domestic pig has become the model corpse for carrion research (Catts and Goff 1992; Goff 1993). Payne went on to publish several other papers from his groundbreaking work, including reports of arthropods from buried and submerged carcasses (Payne et al. 1968; Payne and King 1972).

Beginning in the 1940s, several forensic practitioners, including Marcel Leclercq, Pekka Nuorteva, Bernard Greenberg, and M. Lee Goff, began to publish their case reports that identified promising insect taxa for estimating the postmortem interval in death investigations (Leclercq and Quinet 1949; Nuorteva et al. 1967; Greenberg 1985; Goff and Odom 1987; Goff et al. 1988). These forensic developments gave renewed purpose to carrion research, including the creation (in 1980) of the first outdoor laboratory for human decomposition research (Shirley et al. 2011), but no study had tested ecological mechanisms for the succession patterns observed. Over the next 75-plus years, however, carrion would become the focus or model for investigating other ecological concepts and theories, such as detrital food webs (Reed 1958; Cornaby 1974; McKinnerney 1978; Schoenly and Cohen 1991), successional dynamics (Beaver 1977; Schoenly and Reid 1987; Boulton and Lake 1988; Moura et al. 2005), energetics of animal decomposition (Putnam 1978a,b), spatial dynamics (Kneidel 1985; Hanski 1987; Ives 1991; Fiene et al. 2014), resource pulses (Yang 2006), nutrient cycling (Carter et al. 2007; Parmenter and MacMahon 2009), and landscape heterogeneity (Barton et al. 2013).

It was also during the 20th century that the stage-based paradigm emerged in carrion ecology and forensic entomology. Successional timetables, which displayed the names and occurrences of different insect species and their life stages over time, included decay stages that were named according to observed physical and chemical changes in the carcass. In these early ecological studies, stage descriptions varied in both number and duration. For example, Fuller (1934) described three stages, Reed (1958) described four, Bornemissza (1957) described five, and Payne (1965) described six. One widely held belief was that the onset of each stage was marked by abrupt changes in insect composition (Schoenly and Reid 1987), similar to Mégnin's (1894) notion of "squads" and Clements' (1916) "seres." For example, Fuller wrote:

> It has become obvious, as Mégnin [1894] pointed out, that each stage of decomposition is characterized by a particular group of insects, but the process of decomposition itself is largely dependent on the presence of the insects (Fuller 1934:24).

Some carrion researchers even used the terms "microsere" and "microseral stages" from plant succession studies to document decomposition progress (e.g., Reed 1958; Johnson 1975). The stage-based paradigm was first challenged by Schoenly and Reid (1987) who demonstrated that succession in 11 published studies (largely) followed a continuum of gradual changes, verifying the existence and timing of authors' decay stages in only a minority of cases. Those conclusions were later corroborated by Boulton and Lake (1988) and Moura et al. (2005). Despite these findings, and a reminder by Peters (1991) that decay stages represent typological thinking, their use has spread in the forensic literature (i.e., entomology, anthropology, taphonomy). Practitioners have used them as "convenient descriptors" for summarizing postmortem changes (e.g., Mann et al. 1990; Anderson and VanLaerhoven 1996; Tibbett and Carter 2009) or as "reference points" for educating judges and juries in the courtroom (Goff 2000). Moreover, just like the individualistic and continuum views for plant communities championed by Gleason and Ramensky, the richness, abundance, and distribution of chemical compounds emanating from a decomposing carcass interact in complicated ways, are dependent on the physical environment, and rarely coincide with established decay stages, yielding limited use as indicators of decomposition (Vass et al. 1992; Vass 2012). Although some authors who have used decay stages have acknowledged their artificiality, using them still evokes a stepwise (and necessarily abrupt) view of carcass decay that misinforms the more continuous process. The widespread adoption and uncritical acceptance of decay stages in carrion research has unfortunately diverted attention from empirical testing of ecological mechanisms and models.

The descriptive era brought increased ecological attention to carrion (e.g., Elton and Miller 1954) but did little to advance understanding of temporal dynamics. Forensic entomology and carrion ecology continue primarily as descriptive disciplines (Michaud et al. 2012), although a shift has begun toward a more hypothesis-driven framework (see below).

CONNECTIONS BETWEEN PLANT AND CARRION SUCCESSION THEORY

MULTIPLE INDEPENDENT DISCOVERIES

Multiple independent discoveries, according to Lamb and Easton (1984), have occurred in every branch of science and involve researchers working in different laboratories and countries who were unaware of each other's contributions. In addition, multiple discoveries are often dependent on common precursors, such as the theory of evolution by natural selection in which Darwin and Wallace were inspired by the economic theories of Thomas Malthus (Lamb and Easton 1984). In the case of ecological succession, we show that carrion succession theorists (i.e., medical examiners and forensic entomologists) of the late 1800s (i.e., Mégnin, Yovanovitch, Johnston, Villeneuve, Motter, Niezabitowski) preceded plant succession theorists (i.e., Cowles, Clements, Gleason, Ramensky) by two decades in formalizing and testing this concept. Inspection of the footnotes and bibliographies of the papers on succession by Cowles and colleagues do not include the papers and books of Mégnin and colleagues. Moreover, the papers from Cowles and colleagues referred only twice to carrion-related terminology or succession in carrion. In one instance, Cowles used "corpses" to describe once buried and resurfaced pine trees in retreating dunes (Cowles 1899:298). In the second, Clements linked "cadavers" with seres when describing examples of "miniature successions that run their short but somewhat complex course within the control of a major community" (Clements 1936: 280), but provided no citation with this description. Despite carrion and plant ecologists having different historical roots (i.e., forensic medicine and plant geography, respectively), they did depend on common precursors that could have provided building blocks for developing parallel succession concepts. For example, both groups cited studies that refuted spontaneous generation, namely, Redi (1668) by carrion ecologists and Thoreau (1860) by plant ecologists. Also, both groups depended on the binomial classification system of Linnaeus (and the work of other systematists) and benefited from the emergence of specialized subdisciplines within botany and zoology (Farber 1982) to describe temporal and spatial changes in species composition. Unlike Mendel's paper on particulate inheritance that went unnoticed for 35 years until it was rediscovered in 1900, we found no evidence that the papers and books of Mégnin and colleagues were rediscovered (i.e., cited) by plant ecologists generations later. This result is not surprising given a persistent divide that has existed for decades between plant and animal ecologists (McIntosh 1985).

Among the first plant ecologists to draw attention to animal-driven succession was Whittaker when he wrote:

> The most effective demonstrations of the manner in which populations succeed one another are in such short-range, small-scale successions as those of infusions . . ., carrion . . ., rotting logs and stumps . . ., dung . . ., etc. (Whittaker 1953:43).

At the time, carcasses were already an overlooked ecological unit (Allee et al. 1949; Elton and Miller 1954) and for the most part were ignored by plant ecologists. Similarly, post-1950s carrion researchers, while introducing or reviewing succession, rarely included the contributions of Cowles and colleagues (but see Schoenly and Reid 1987; VanLaerhoven 2010; Villet 2011). But perhaps most tellingly is that carrion succession's pioneers went uncited by prominent ecology and environmental historians such as Tobey (1981), Egerton (1983, 1985, 2008, 2013, 2014), McIntosh (1985), Worster (1994), and Kingsland (2005). Likewise, medical historians did not cite the contributions of Mégnin and colleagues among the pioneers of forensic medicine and death investigation in Europe and North America (e.g., Smith 1951; Fisher and Platt 1993; Clark and Crawford 1994; Jentzen 2009). Consequently, although common precursors likely contributed to parallel thinking on ecological succession by carrion and plant ecologists, we found no evidence that either group was aware of the other's contributions, at least until the mid-1900s.

Despite having common precursors, we hypothesize that different academic cultures and institutional structures kept carrion and plant ecologists apart. Up to the mid-1700s, scientists (i.e., natural philosophers) could conceptualize grand syntheses of knowledge about the entire world, particularly if they were ambitious, disciplined, and well placed (Farber 1982). This was especially true of naturalist-physicians, such as Linnaeus, whose broad training in the natural and medical sciences (Blunt 2001) allowed him to investigate living systems across taxonomic and ecological boundaries. By the 19th century, the volume of information (including collected specimens) had exploded, favoring the proliferation of natural history museums and outlets for publishing (Farber 1982). In this era, "ecology," as coined by Haeckel in

1866, had progressed to become a fusion of natural history and physiology (Farber 1982; McIntosh 1985) and, together with Darwin's theory of evolution in 1859, should have forged robust and lasting collaborations between carrion and plant ecologists. But by the turn of the 20th century, when carrion and plant ecologists were investigating succession, the acceleration of scientific information led to specialization and compartmentalization of professions and institutions (Smith 1951; Farber 1982; McIntosh 1985). In North America, the birthplaces for ecology developed around botany programs, such as the Carnegie Institution of Washington's Desert Botanical Laboratory and the New York Botanical Garden that pursued mostly plant taxonomy, genetics, and ecophysiology (Kingsland 2005), land-grant universities in Nebraska, Iowa, and Kansas (among others) that trained generations of grassland ecologists (Tobey 1981), and private universities such as the University of Chicago that trained both plant and animal ecologists (McIntosh 1985). Consequently, in the early 1900s, American ecologists mostly saw themselves as botanists and zoologists (Kingsland 2005) and rejected attempts by their leaders to embrace a broader research agenda (Huntington 1920; Moore 1920; Clements 1935) that included human-centered disciplines (e.g., public health and urban ecology; Kingsland 2005). Following this trend, the journal *Ecology* became more narrowly focused on botanical topics through the 1920s (Kingland 2005). Over the same time period, but independently of these developments, the emergence of forensic pathology, as a medical specialty, into death investigation had begun in America in the late 1800s (Fisher and Platt 1993). But even before this time, the coroner system, made up of elected persons who typically had no medical training to investigate untimely deaths, was legislated into American colonial governments as early as 1777 (Hanzlick 2007). By the early 1900s, the modern medical examiner system had been established, and a trend to replace untrained coroners with physician medical examiners (expertly trained to perform death investigations and autopsies) had begun (Hanzlick and Combs 1998). However, conflicts continue today between medical examiners and coroners, and with politicians and law enforcement, resulting in a patchwork of death investigation systems at state and local levels (Hanzlick 2007; Jentzen 2009). Consequently, as a result of specialization and compartmentalization, newly established American institutions and curricula in ecology and medicine did much to weaken the potential for interdisciplinary collaboration, not just between plant and carrion ecologists, but between plant and animal ecologists. As Lamb and Easton (1984) have observed, most scientists do not pursue interests or advance theories beyond their cultural boundaries, but instead adopt the values of the society of which they are part.

Finally, we hypothesize that carrion and plant ecologists had different objectives and motivations that worked against mutual recognition and exchange of ideas on ecological succession. First, plant ecologists have mostly studied succession prospectively (Kingsland 2005) as a forecasting tool to predict future changes in community composition, whereas carrion ecologists (particularly those who did casework) studied succession retrospectively, backtracking egg laying by adult flies and beetles to estimate time of death of the deceased (Byrd and Castner 2010). This may partly explain why Markov chain models of succession, used mostly by plant ecologists for analyzing future successional states, have found little appeal among carrion ecologists (i.e., "the forward problem"; Solow and Smith 2006). Second, plant succession is a concept embedded within the ecosystem (Tobey 1981; McIntosh 1985; Kingsland 2005); as such, most early plant ecologists held that ecosystems (through their communities) exhibited large-scale homogeneity and long-term stability, rooted in the "balance of nature" assumption that prevailed for centuries (Wu and Loucks 1995). In contrast, carrion was viewed and studied in isolation of the larger ecosystem, provoking early animal and carrion ecologists to use the terms "microsere," "microseral stage," and "microcommunity" to describe these habitat patches (Allee et al. 1949; Reed 1958; Payne 1965; Johnson 1975). Despite these different perceptions, a few early and far-sighted plant ecologists (McIntosh 1985) recognized the linkage between ecosystem heterogeneity and scale multiplicity (i.e., hierarchical patch dynamics; Wu and Loucks 1995). One was William S. Cooper, who concluded after mapping and aging trees in Isle Royale, Lake Superior, that the forest is a:

> mosaic or patchwork [that] changes continually in a manner that may almost be called kaleidoscopic when long periods of time are considered (Cooper 1913:36).

Decades later, Alexander S. Watt, while expanding on this framework, introduced the term "gap phase" when describing patches of forest (Watt 1947:12) and cited insect inhabitants of decaying walnuts, logs, and dung as animal examples (Watt 1947:20). Third, most 20th-century plant and animal ecologists chose to study "pristine" environments that were largely (although never entirely) removed from human activities (Kingsland 2005); whereas, many carrion ecologists conducted their field work in and around human-managed landscapes (e.g., agricultural experiment stations, urban and suburban areas, landfills). Fourth, most academic ecologists have historically shunned involvement in environmental litigation because they perceived it to be unprofessional, claimed it diluted their objectivity, and found it brought few academic rewards (Willard 1980). In contrast, many carrion ecologists (i.e., forensic entomologists, anthropologists, taphonomists) have routinely assisted law enforcement and testified as expert witnesses (e.g., Haglund and Sorg 1997; Greenberg and Kunich 2002; Dupras et al. 2006). Tellingly, these ideological and motivational differences are reflected in textbook comparisons that show a conspicuous lack of environmental litigation coverage in general ecology textbooks (even cases involving plant succession and biodiversity; see Willard 1980), compared to whole-chapter coverage of litigated casework, expert witness testimony, and/or courtroom practices in many forensic entomology, anthropology, and taphonomy textbooks (e.g., Haglund and Sorg 1997; Greenberg and Kunich 2002; Burns 2013).

To sum up, the available evidence shows that carrion and plant ecologists of the late 19th and early 20th centuries, despite having common precursors, advanced ecological succession theory in isolation and developed different academic cultures, motivations, and objectives that kept them apart. It is tempting to speculate whether the origin and history of this theory would have unfolded differently if specialization and compartmentalization of the natural and medical sciences in the late 19th century had been delayed, or if early plant and animal ecologists and their founding institutions in the early 20th century had coalesced and broadened their scope, or if plant and carrion ecologists in the mid-20th century had shared similar views of the ecosystem and in the way they studied succession. Although these alternate histories will remain thought experiments, it seems clear that the origin and development of ecological succession theory unfolded as a series of missed opportunities for cross-collaboration between its two groups of pioneers and successors.

CARRION INSECT SUCCESSION: A CLEMENTSIAN OR GLEASONIAN PROCESS?

Since the theoretical framework of carrion-insect succession does not provide many answers with regard to community assembly, it is tempting to draw information from plant ecology. Carrion use by insects appears to evoke agreement, in part, with both Clementsian and Gleasonian succession. From a Clementsian view, carrion-insect succession is directional in nature and is relatively predictable within a given ecosystem of a biogeographic zone (e.g., Anderson 2010), two traits that are required for time-since-death estimation. Although decomposition is marked by statistically predictable stages or "seres" (Michaud and Moreau 2011), boundaries between stages (Schoenly and Reid 1987; Boulton and Lake 1988; Moura et al. 2005) and between ecosystems (Michaud et al. 2010) rarely correspond to abrupt changes in arthropod composition. For that reason, carrion-insect succession also evokes comparison with

Gleasonian succession. Another Gleasonian trait is interannual variation in insect arrival and departure times that occur when carcasses are exposed in the same seasons and environments in different years (e.g., Archer 2003; Michaud and Moreau 2009). Also, some insect species that frequent carrion have a random occurrence pattern and do not appear to follow the predicted successional sequence (Michaud and Moreau 2009).

Plant and carrion-insect succession also differs in major and obvious ways. Carrion functions as a nonequilibrium island (Beaver 1977) that is without primary production or a climax assemblage because its successional endpoint is recycling of the remains into gravesoil (Poole 1974; Braack 1987; Begon et al. 1996; Carter et al. 2007). In her analysis of turnover rates, Anderson (2007) examined successional data sets from both plant and carrion communities and found that the main drivers of succession were competition, abiotic limitation, and dispersal limitation, and concluded that her results were more consistent with a Gleasonian approach for plants but could not come to any conclusion with respect to carrion-insect succession. Evidence from dispersal studies on saprophagous Diptera and Coleoptera, however, show that they have wide dispersal ranges that span several kilometers (see references in Michaud et al. 2012). Moreover, competition among fly larvae on carrion, dung, and fallen fruit has been well documented (e.g., Valiela 1974; Denno and Cothran 1975; Atkinson and Shorrocks 1984; Kneidel 1984; Hanski 1987; Ives 1988); however, the net effect of competition on the rest of the insect community remains unknown. Although these studies provided important insight on how community assembly proceeds on ephemeral and divided resources, none directly explored mechanisms of succession. More field studies will be needed to reach a conclusion about whether carrion-insect succession fits the Gleasonian model, the Clementsian model, or if it is a unique process deserving its own conceptual framework.

FUTURE QUESTIONS IN CARRION ECOLOGY AND FORENSIC ENTOMOLOGY

WHAT MECHANISMS UNDERLIE CARRION-INSECT SUCCESSION?

The Gleason versus Clements debate is likely to persist for many years to come. This is because these concepts are rooted in theory rather than empirical data, which defies straightforward testing. Connell and Slatyer (1977) attempted to resolve the testability issue by proposing three mutually exclusive mechanisms of succession (facilitation, inhibition, and tolerance) for plants and sessile aquatic animals. Facilitation has been proposed as a likely mechanism for animal succession on carrion (Connell and Slatyer 1977; Schoenly and Reid 1987), although no empirical evidence was offered to support this claim. Connell and Slatyer wrote:

> The mechanisms of the facilitation model probably apply to most heterotrophic successions of consumers feeding on carcasses, logs, dung, litter, etc. . . . No experimental investigation has been carried out to demonstrate the details of the process, but the evidence seems to support the application of this model (Connell and Slatyer 1977:1124).

Later, Schoenly and Reid wrote:

> The species replacement patterns . . . are consistent with Connell and Slatyer's (1977) "facilitation" mechanism (model 1) of community succession . . . We stress, however, that the available data sets are inappropriate for testing the facilitation hypothesis. Corroboration of this hypothesis will require further field and/or laboratory trials (Schoenly and Reid 1987:199).

Over a decade later, Smith and Baco (2003) stated in their review of whale falls at the deep-sea floor that facilitation was the dominant mechanism in community assembly, although again the hypothesis was not directly tested. Researchers working on other degradative habitats where facilitation has been demonstrated, such as rotting wood (Renvall 1995; Weslien et al. 2011) and dung (Slade et al. 2007), also hinted that facilitation may occur on carrion. However, as Schoenly and Reid (1987; see above) pointed out almost 30 years ago, further testing will be required to better understand how applicable to carrion facilitation (or any other mechanism) truly is.

Another untested assumption dates back to Mégnin (1883, 1887, 1894) and his concept of "squads" in which he proposes that carrion-insect succession is driven by physical-chemical changes in cadaver decay (Figure 1). In other words, different waves of insects are attracted to specific odors as they are released sequentially during decomposition. A few studies have identified many compounds that are released during carcass decomposition (e.g., Vass et al. 1992; Vass 2012) and the response of carrion-associated insects to certain compounds has been shown (e.g., Frederickx et al. 2012; von Hoermann et al. 2012; Johansen et al. 2014); however, we are aware of no study that has established a link between chemical succession and insect succession in carrion. Indeed, Vass (2012) has proposed an "odor signature" for human decomposition that may have many potential benefits for the forensic sciences. However, such a concept, if it can be linked with corpse-insect succession, will require further experimentation in controlled settings.

Succession is a leading concept in ecology (Cherrett 1989) and its predictability in carrion is a basic premise behind forensic entomology. Focusing more time and effort on mechanisms of succession is likely to increase our understanding of community assembly and improve the theoretical framework of both carrion ecology and forensic entomology. Despite these knowledge gaps, researchers cite the potential of carcasses to illuminate ecological principles, in large part, due to their discrete and ephemeral nature and ease with which they can be acquired, replicated, manipulated, and sampled (Braack 1987; Schoenly and Reid 1987; Finn 2001). Because carrion communities assemble from a regional species pool, they offer realistic diversity gradients (and endless community combinations) for investigating diversity-ecosystem function relationships (Finn 2001). Moreover, the hotly disputed space-for-time substitution (Pickett 1989; Johnson and Miyanishi 2008; Walker et al. 2010) does not apply, giving carrion a clear advantage as a model system for investigating mechanisms of succession and other ecological processes.

DEVELOPING THE ECOLOGICAL FRAMEWORK OF FORENSIC ENTOMOLOGY

Historically, the forensic sciences were held in high regard by the public and the courts throughout most of the 20th century. However, the landmark paper by Saks and Koehler (2005) and the long-anticipated, congressionally mandated National Research Council (NRC 2009) report, *Strengthening Forensic Science in the United States: A Path Forward*, drew attention to many scientific inadequacies of the forensic identification disciplines (e.g., fingerprinting, toolmarks, ballistics). Among the 13 recommendations in the NRC report was the need to:

> develop tools for advancing measurement, validation, reliability, information sharing, and proficiency testing in forensic science and to establish protocols for forensic examinations, methods, and practices (NRC 2009:214; Recommendation 6).

Although forensic entomology was not a target of the report, a paradigm shift to correct methodological shortcomings and develop theoretical models had started before the report was published. For example, forensic entomologists had anticipated the need to incorporate null models and Monte Carlo methods in hypothesis testing (Schoenly 1991, 1992; Schoenly et al. 1996), develop probability-based estimates of time since death (Wells and LaMotte 1995; LaMotte and Wells 2000; Michaud and Moreau 2009), test the reliability of pig carcasses as model corpses (Schoenly et al. 2007), and conduct blind validation tests of time-since-death methodology (VanLaerhoven 2008). After the report was published, researchers in the field realized the need to design better field experiments (Michaud et al. 2012; Michaud and Moreau 2013) and improve and field test their statistical models (Michaud and Moreau 2011; Basqué and Amendt 2013; Perez et al. 2014). Carrion ecologists, in turn, have vowed to develop the ecological framework of forensic entomology by proposing a strategy that unifies basic and applied decomposition research (Tomberlin et al. 2011a,b). Similarly, carrion ecologists have highlighted the importance of decomposing carcasses in the larger ecosystem in an attempt to advance carrion ecology theory. For example, Parmenter and MacMahon (2009) examined the decomposition rate of several vertebrate species for different seasons and microsites and also measured energy and nutrient loss through nutrient cycling and compared these loss rates to plant-litter studies. Yang et al. (2008) proposed that pulsed resources, such as carrion, influence ecological processes at the individual, population, and community levels. Barton et al. (2013) developed a framework of carrion dynamics that weds succession theory with aggregation and coexistence theory (e.g., Atkinson and Shorrocks 1984; Ives 1988) and suggested refocusing future research on carrion's impacts on biodiversity and ecological processes at different spatial scales. Pechal et al. (2014) showed how insect access to carrion, if delayed by biophysical or forensic factors, can shift community structure and arrival patterns, and slow decomposition rates. Although much work needs to be done to elucidate mechanisms of carrion-insect assembly, armed with this new paradigm, carrion ecologists and forensic entomologists have the momentum, tools, and ecological mindset to accomplish it.

CONCLUSION

At a time when most ecologists believed that plants directed succession, Elton (1927) warned plant ecologists that they should not ignore animals, and offered examples of how activities of animals (e.g., eating, dispersing, trampling, and destroying vegetation) could influence successional outcomes (Cain et al. 2008). Today, authors of ecology textbooks feature examples of both autogenic (plant) and heterotrophic (marine, degradative) succession, but often ignore carrion-arthropod succession as an example of the latter (but see Begon et al. 1996; Krebs 2009). Here we showed that not only did early forensic entomologists advance and test the first formal definition and mechanism of ecological succession (Mégnin 1883, 1887, 1894; Yovanovitch 1888; Johnston and Villeneuve 1897; Motter 1898; Niezabitowski 1902), but that their history and contributions paralleled those of early plant ecologists. For example, both groups originated in Europe, used succession-related concepts to refute the theory of spontaneous generation, and introduced succession to colleagues in North America. Both groups also initially placed great importance on typological concepts (i.e., "seres" in plant ecology, "squads" in carrion ecology), the role of site and climate in shaping successional outcomes, and offered a qualitative framework of the mechanisms involved. Afterward, for nearly a century, empirical testing of succession mechanisms in carrion went underexplored, due in large part to an emphasis on insect taxonomy and observational studies (Michaud et al. 2012) and to the lingering, untested claim that facilitation was the sole mechanism (Connell and Slatyer 1977; Schoenly and Reid 1987; Smith and Baco 2003). Today, the Clementsian (i.e., stage-based) view remains dominant in carrion ecology and in several forensic disciplines (i.e., entomology, anthropology, taphonomy), and momentum is growing to put these disciplines on a more ecological (and empirical) footing. We expect that the theoretical framework of these forensic disciplines will benefit greatly from ecology-based (i.e., mechanistic) thinking, much in the same way modern ecology will benefit from increased understanding of successional dynamics on carrion.

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