
Trends in Ecology & Evolution
Trends Ecol. Evol. February 2011 Vol. 26 No. 2, pp. 53–104 ISSN 0169-5347
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# Basic research in evolution and ecology enhances forensics

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**In 2009, the National Research Council recommended that the forensic sciences strengthen their grounding in basic empirical research to mitigate against criticism and improve accuracy and reliability. For DNA-based identification, this goal was achieved under the guidance of the population genetics community. This effort resulted in DNA analysis becoming the 'gold standard' of the forensic sciences. Elsewhere, we proposed a framework for streamlining research in decomposition ecology, which promotes quantitative approaches to collecting and applying data to forensic investigations involving decomposing human remains. To extend the ecological aspects of this approach, this review focuses on forensic entomology, although the framework can be extended to other areas of decomposition.**

## Forensic entomology

Forensic entomologists analyze arthropod evidence collected from decomposing remains to estimate the initial time of arthropod colonization, yielding a minimum postmortem interval (Box 1 [1]). To form these estimates, entomologists rely on laboratory studies that document arthropod development as well as described patterns of arthropod succession on carrion in the field. This discipline is an application of community and evolutionary ecology. It requires a working knowledge of a basic process (decomposition) and the ecological and evolutionary forces that affect variability in that process. Understanding biological variation is crucial to community and evolutionary ecology studies for mechanistic reasons. The same can be said for forensics as 'variability' is equivalent to 'error'. Thus, understanding how factors influence variability in decomposition can reduce the degree of error in predictions of a postmortem interval.

## Conceptual framework based on principles of ecology and evolution

Past attempts to streamline research in decomposition biology have not linked community and evolutionary ecology to forensics. Payne [2] identified stages of decomposition based on the structure of the arthropod community colonizing carrion. This approach focused on the remains, usually independent of the surrounding ecosystem, and did not address the ecological mechanisms of the process. Although initially useful for forensic applications, this paradigm is too observational to yield advances in forensics. More recently, Yang [3] defined 'resource pulses', which includes carrion, and described their causes and effects within a larger ecosystem context. However, this work does not provide a framework for estimating the time of death of individual carcasses. By organizing the process of decomposition in discrete terms, the framework proposed by Tomberlin *et al.* [1] links concepts such as those described by Payne (i.e. arthropod succession on ephemeral resources) and Yang *et al.* (i.e. interactions of those resources with surrounding ecosystems). Studies using this framework will be useful for meta-analyses and, when applied in forensic investigations, could lead to more accurate estimates of the minimum postmortem interval for human remains [1].

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## Ecology of decomposition related to forensic entomology

Decomposition is fundamental to ecosystem function through nutrient and energy cycling, food webs, nutrient pulses and facilitating community assembly [3,4]. One important area of carrion research as related to community assembly is the identification of factors that lead insects to colonize remains, including potential insect–microbe interactions [5]. However, the processes and mechanisms of these interactions as they contribute to ecosystem function are insufficiently studied [3], even though communities associated with carrion are thought to undergo predictable succession patterns [1].

Investigators typically initiate data collection at the time of arthropod colonization [2,4], omitting valuable data about the period extending from death until colonization (the precolonization interval, Box 1). Consequently, little is known about the ecological interactions and evolutionary drivers dictating community assembly that have direct bearing on predictions of the postmortem interval. Many of these concepts are understood by ecologists, but their application to forensics remains unclear, and innovative studies using these concepts are warranted for improving forensics.

## Molecular and evolutionary genetics

Ecological genetics concerns the inheritance of phenotypes contributing to the fitness of an organism in its environment [6], including life history, behavioral and reproductive characteristics. Such traits are implicit throughout the proposed framework (Box 1) and an understanding of their genetic architecture will lead to less error associated with postmortem interval estimates. For example, the presence of a microbe that inhibits blow fly

**Box 1. A framework for using knowledge of the ecological and evolutionary processes of decomposition over time to improve the scientific basis of forensic entomology**

The framework (Box 1, Figure Ia [1]) considers two intervals of colonization, each with specific phases of biological activity that can be identified and used in formulating specific hypotheses related to ecological and evolutionary drivers of carrion decomposition. This basic information can be used to test and validate estimates of parameters, such as the period of insect activity in relation to the postmortem interval when arthropods are used as evidence in criminal investigations. The framework is purposefully elastic, with each interval and phase dependent on the study organism(s) and abiotic factors targeted in a study.

The pre-colonization interval begins at death and extends to colonization by arthropods. The length of this interval varies depending on the abiotic and biotic conditions, including the target arthropods being studied. Although this interval has consequences for the evolution and ecology of relevant species, it is poorly studied.

The exposure phase begins at death and continues until the remains have been detected by arthropods either visually or through olfaction.

The detection phase comprises two stages: (i) activation, which involves detection by the target arthropod; and (ii) searching, which is the behavioral response of the arthropod to the stimulus originating from the remains. Many ecological studies that have examined carrion as it relates to patchy resources and coexistence have addressed this phase but not under the context presented. Some studies have also linked detection with the post-colonization interval as it relates to ecological and evolutionary issues (e.g. priority effects).

The acceptance phase extends from the target arthropod physically contacting the decomposing remains to actual colonization by itself or its offspring.

The post-colonization interval is the most-studied interval in decomposition research. This interval involves extensive colonization, physical contact and consumption of the remains by the target arthropod or its offspring.

The consumption phase is initiated when arthropod adults or larvae begin to feed on the remains. This phase has been studied as part of food-web dynamics and species interactions. However, these studies are often restricted to two-way competitive interactions that are not necessarily indicative of multiple species competing for a decomposing resource in nature. Studies of the quantitative and functional genetics of development time and body size are also needed.

The dispersal phase involves arthropod departure from the remains. Community assembly studies examining nutrient flow through trophic levels are affected by this stage and would have a role in understanding ecosystem processes and food-web interactions. This phase is also crucial to studies of population dynamics within communities. This basic information can be used to test and validate estimates of parameters, such as the period of insect activity in relation to the postmortem interval when arthropods are used as evidence in criminal investigations.

Ecology and evolution both influence decomposition processes (Figure Ib). For any phase or interval in the decomposition process, ecological factors (both abiotic and biotic) can influence the evolution of phenotypes relevant to its initiation and/or duration. Such knowledge should be used to develop predictive models of decomposition that can be used to estimate a postmortem interval.

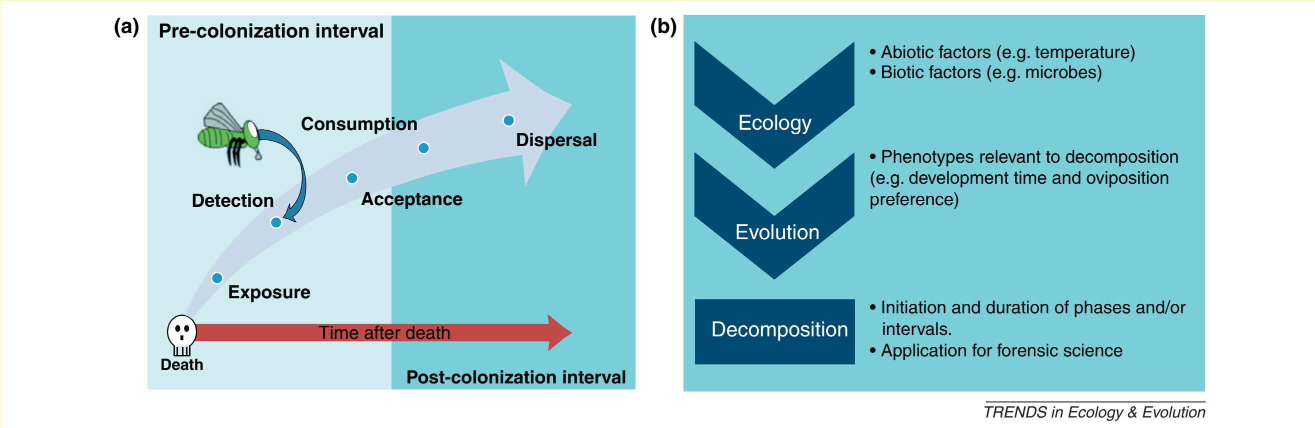


**Figure I.** The process of decomposition is influenced by ecological and evolutionary processes. **(a)** Arthropods are attracted to, and consume, remains in a predictable fashion that can be used to estimate the age of the remains. **(b)** Ecological conditions can cause forensically relevant traits to evolve, contributing to error in forensic predictions.

oviposition on carrion will lengthen the pre-colonization interval (Box 1).

To estimate the minimum postmortem interval, forensic entomologists often rely on the development time and body size of immature flies. These two ecologically important phenotypes are explicit components of the consumption phase of the proposed framework. Although quantitative genetic variation in these traits is observed in other fly species [7–9], there is little overt reference to quantitative genetic concepts in the forensic entomology literature and a paucity of studies devoted to understanding the inheritance of development time and body size. A central concept in quantitative genetics is that there are genetic and environmental contributions to such traits [6,10]. Furthermore, genotypes can interact with the environment, leading to locally adapted populations [6]. Any of these factors can affect variation in forensically informative traits.

Forensic entomology is replete with examples of environmental effects on blow fly development, but few forensic entomology studies explicitly acknowledge that they are studying plasticity [11]. The continuation of plasticity research in forensic entomology is crucial to future success, as environmental effects might explain differences in development time observed among studies characterizing the same species [11]. Any environmental effects on arthropod phenotypes are important sources of variation that must be studied to limit error in postmortem interval estimates.

Population differences in forensically important insect phenotypes are understudied, although they have been hypothesized [12,13]. One study has established different development rates for separate populations of a forensically important species raised in a common environment [14]. It demonstrated that predictions of blow fly age, based on development data from the wrong population, can result in a greater than 10% error in postmortem interval estimates [14]. Such errors can result in wrongful convictions or exonerations in the court room.

It will be necessary to identify relevant genetic markers of populations in which phenotypic differences are observed, and population and functional genetic approaches can be used to identify markers. There are few applications of population genetics in forensic entomology (e.g. [15]) and functional genetic research is still in its infancy [16]. However, recent technical advances enabling affordable genomic studies in non-model organisms [17] should simplify efforts to identify neutral and functional markers of variation in forensically informative phenotypes. Finding indicators of quantitative genetic differences will be central to understanding the relationship between forensically and ecologically relevant traits of necrophilous insects and the duration of each phase of decomposition (Figure Ib).

## Conclusion

This article was written to stimulate intellectual interactions and collaborations among disparate groups of scientists. Forensic scientists are implored to consider community and evolutionary ecology concepts when designing experiments and interpreting data. We ask evolutionary ecologists to provide constructive input to a *de facto* daughter discipline, just as population geneticists provided the important intellectual guidance that enabled DNA analysis to become the gold standard of the forensic sciences.

A framework (Box 1) has been proposed for decomposition studies in forensic science based on principles of evolution and ecology, aligning the field with basic research in classic areas of research such as community assembly and phenotype prediction. The terminology is consistent throughout, supporting multidisciplinary approaches to understanding the scientific foundation and application of decomposition ecology in forensics. This framework, or others like it, will be instrumental in meeting the requirements of the 2009 National Research Council report [18].

## Acknowledgments

The Department of Entomology and Agrilife Research at Texas A&M University provided financial support to A.M.T. and J.K.T. The University of Dayton Research Council provided financial support to M.E.B. We would like to thank J.S. Johnston, P. Adler, M. Slotman, M. Eubanks, S. Nuzhdin and R. McEwan for comments on earlier versions of this article.

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doi:10.1016/j.tree.2010.12.001 Trends in Ecology and Evolution, February 2011, Vol. 26, No. 2