REVIEW

Detritus, trophic dynamics and biodiversity

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Abstract

Traditional approaches to the study of food webs emphasize the transfer of local primary productivity in the form of living plant organic matter across trophic levels. However, dead organic matter, or detritus, a common feature of most ecosystems plays a frequently overlooked role as a dynamic heterogeneous resource and habitat for many species. We develop an integrative framework for understanding the impact of detritus that emphasizes the ontogeny and heterogeneity of detritus and the various ways that explicit inclusion of detrital dynamics alters generalizations about the structure and functioning of food webs. Through its influences on food web composition and dynamics, detritus often increases system stability and persistence, having substantial effects on trophic structure and biodiversity. Inclusion of detrital heterogeneity in models of food web dynamics is an essential new direction for ecological research.

Keywords

Decomposers, detritus, diversity, ecosystems, food chain, food web, primary productivity, processing chains, subsidies, trophic dynamics.

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INTRODUCTION

Most primary production is not consumed by herbivores, but rather is returned to the environment as detritus to play critical roles in organizing and sustaining ecosystems (Wetzel 1983; Cyr & Pace 1993; Hairston & Hairston 1993; Polis & Strong 1996; Crawley 1997). Over extreme time-scales, the distribution, sequestration and decomposition of detritus, particularly structural materials, has arguably affected the current and past stoichiometry of living biota and the biogeochemical cycles within the biosphere (Reiners 1986). In the more immediate time-scales, detritus affects the trophic structure and dynamics of communities, has the potential to support a greater diversity of species and support larger predator biomass and longer food chains than would be supported by living autotrophs alone (Hairston & Hairston 1993), may stabilize both energy flux and the dynamics of consumer populations, may alter energy and nutrient transfer efficiencies across trophic levels and increase species persistence and food web stability in model configurations that are otherwise unstable. In addition to its effects on trophic structure and dynamics, detritus also physically alters habitats (Schindler 1990; Williamson *et al.* 1999), facilitating some species and inhibiting others (Harmon *et al.* 1986; Facelli 1994; Peterson & Pickett 1995). Moreover, the naturally evolved differences and human

induced alterations in material fluxes between pools of detritus, living organisms, and inorganic nutrients have had global consequences with respect to carbon storage, nutrient translocation, environmental pollution, and climate change (Cebrian & Duarte 1995). Given its central role in community organization, why has much of ecological theory been based on models that include living matter alone?

The answer is not that detritus has been ignored, as ecologists have included detritus in the descriptions of communities and ecosystems, and extensively described it and fate its in ecosystems (Forbes 1887; Summerhayes & Elton 1923; Elton 1927; Lindeman 1942; Swift *et al.* 1979). Much of the early descriptive work alluded to detritus, if not by name, by including 'dead plants', 'decaying matter', 'dung', or 'litter'. When Lindeman (1942) proposed the concept of food chains in lake ecosystems, his consideration of detritus (which he termed 'ooze') marked a significant departure from contemporary thinking (see Fig. 1 in Lindeman 1942) as the work was pivotal in recognizing detritus as central to energy flow within ecosystems. Teal (1962) and Odum (1969) emphasized the importance of detritus in supporting food webs, leading to an ecosystem framework that compartmentalized trophic interactions and energy flow in food webs into a grazer pathway, where energy originates from living primary producers, and a detritus or decomposer pathway, where energy originates
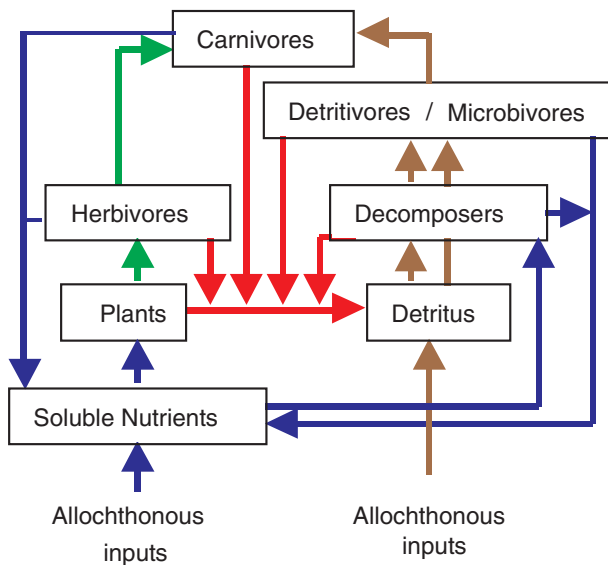
Figure 1 Features of a generalized food web that incorporates detrital dynamics, both as allochthonous imports into the web and autochthonous internal cycling within the web. The green arrows represent the flow of matter through the grazer pathway that originates from primary producers (plants or algae). The brown arrows represent the decomposer pathway, that originates from detritus (external imports and internal pools). The red arrows depict the autochthonous flow of matter to the detritus pool that results from death of all living organisms and from unassimilated prey. The blue arrows signify the mineralization and immobilization of soluble nutrients.

from dead organic matter. Later work by Wetzel (1983) and Odum & Biever (1984) emphasized that the majority of energy in many food webs flows through detrital pathways.

Although ecology, and particularly ecosystem ecology, has a long tradition of including detritus in its discussion, and much has been formalized about the origins and transformations of detritus, it is the theories of food webs and trophic dynamics that have largely neglected detritus. The reasons for the omissions appear largely historical, tracing back to early modelling efforts by Lotka (1925) which focused on living organisms, and then to the schism of thought that developed between the organism-centric community ecology and nutrient-centric ecosystem ecology in the 1950s. This review incorporates the 'brown-world' of detritus into the largely 'green-world' of food web theory by integrating population, community and ecosystem ecology (Hedin 1991; Pomeroy 1991). In doing so, we demonstrate that many of the fundamental questions of ecology, from the structure of food webs and the length of food chains, to the dynamics of trophic cascades, may have different interpretations when the detritus is included as a central component of an ecosystem. We emphasize that detritus is not homogeneous, but rather is highly variable in form and

distribution expressed at multiple spatial and temporal scales, and that this variability has implications for individual organisms, food webs and ecosystems. Building on the framework developed here, our hope is that future studies can better incorporate and understand this complexity as it impacts local and global ecosystems.

WHAT IS DETRITUS?

Swift *et al.* (1979) provided one of the most comprehensive treatments of detritus, focusing on physical attributes such as size, chemical quality, and its interactions with organisms. Detritus can be broadly defined as any form of non-living organic matter, including different types of plant tissue (e.g. leaf litter, dead wood, aquatic macrophytes, algae), animal tissue (carrion), dead microbes, faeces (manure, dung, faecal pellets, guano, frass), as well as products secreted, excreted or exuded from organisms (e.g. extra-cellular polymers, nectar, root exudates and leachates, dissolved organic matter, extra-cellular matrix, mucilage). The relative importance of these forms of detritus, in terms of origin, size and chemical composition, varies across ecosystems.

Size classifications of detritus, range from simple and complex organic molecules in dissolved organic matter (DOM), to particulate organic matter (POM), plant litter, and coarse woody debris. These size fractions are dynamic, as coarse debris is converted to fine particulate matter, while dissolved forms of detritus are continually leached from all size fractions. Furthermore, via aggregation, dissolved detritus can be resynthesized into particulate fractions and small particulates built up into larger complexes. The nomenclature for size classification is far from standardized. For example, aquatic ecologists subdivide particulate detritus into large particles (coarse POM) and small particles (fine POM). In soil, where it is difficult to separate aged detritus from the soil matrix, density distinguishes more labile ('light fraction' or LF) from the less degradable POM fraction that is incorporated into aggregates, association with clay and silt, and chemical/biological transformation into recalcitrant molecules (Six *et al.* 2002).

Detritus is also categorized by its chemical composition, which reflects its source, its legacy, and the biochemical composition of life forms. These compounds include specialized polymers associated with the cell walls of plants (e.g. cellulose, hemicellulose, lignin), and fungi (e.g. chitin, tannin, melanin), as well as universal biomolecules such as fats/oils, nucleic acids, proteins, other polysaccharides, and the monomeric constituents of these polymers: fatty acids, sugars, amino acids, nucleotides and nucleiosides, fatty acids and other aliphatics, and aromatics. Certain bulk properties of detritus that reflect chemical composition – C : N ratio, lignin content, and nutrient content– are useful predictors of

decomposition of newly deposited detritus (Swift *et al.* 1979; Mellilo *et al.* 1982; Coleman *et al.* 1983).

DETRITUS AS A HABITAT AND HABITAT MODIFIER

Detritus serves as a habitat, e.g. shelters, refugia and breeding sites, is an integral component to the so-called ecosystem engineering activities (*sensu* Jones *et al.* 1994), and modifies the physical structure and conditions of habitats, such as moisture, light, temperature, and flow velocity of wind and water. Decaying organisms can harbour whole food webs with material passing through several trophic levels before completely mineralized. Trees in forests and seagrass and kelp in benthic systems accumulate into detrital piles that provide habitat and food for decomposers (Harmon *et al.* 1986; Romero *et al.* 1994).

In terrestrial systems during soil formation, organisms create and manipulate detritus into complex and stable organic matter (Stevenson 1994), soil aggregates (Jones *et al.* 1994), hydrologic channels (Bardgett *et al.* 2001), and characteristic soil profiles. Mollisols, a soil order (type) typical of grasslands (Brady & Weil 2001), form in large part due to high rates of grass root growth, turnover and exudation, initiating a sequential breakdown of detritus by microbes, protozoa and invertebrates. Extensive bioturbation activity by the grassland soil fauna leads to a well-mixed horizontal profile (Coleman *et al.* 1983). The Alfisols and Spodosols, soil orders that characterize many forested ecosystems, are impacted more by the decomposition of relatively recalcitrant detritus originating from leaves and wood, and the actions of soluble organic acids leached from decaying detritus on soil parent material and organic matter. In each case, the chemical quality of the initial input of detritus and its decomposition products, combined with physical mixing of the detritus by organisms, influence nutrient availability, soil chemistry, and soil architecture that in turn influence species diversity (Brussaard *et al.* 1997).

In pelagic aquatic systems, particulate and dissolved forms of detritus act as physical structures that affect the penetration of light and the temperature within the water column. Many estuaries, reservoirs, large rivers, floodplain lakes, and lakes fed by glacial melt water are turbid because of high concentrations of particulate detritus. The attenuation of light by particulate detritus suspended in the water column reduces photosynthetic rates and reduces the feeding efficiencies of visually-oriented predators. For example, in tropical floodplain lakes, light attenuation by suspended POM mediates piscivorous fish predation, which in turn determines fish species composition (Rodriguez & Lewis 1997). In lakes, DOC decreases photosynthetic radiation and hence reduces primary production, attenuates infrared light (the main source of heat), decreases mixing depths, reduces ultraviolet (UV) light and alters the depth of the thermocline, altering the structure and function of communities in aquatic ecosystems (Schindler *et al.* 1996; Schindler & Curtis 1997; Williamson *et al.* 1999, 2001).

DETRITUS IN FOOD WEBS

Detritus is a source of energy and nutrients to living organisms in most food webs (Fig. 1). Moore & Hunt (1988) deconstructed the 40 community food webs compiled by Briand (1983) into 138 pathways or 'energy channels' that originated with a basal resource (e.g. detritus, primary producers, or consumers) and ended with a top predator. The majority (72.5%) of the community webs contained both detritus and primary producer (*aka* grazer pathway) energy channels in their description that were linked by consumers. Of the 138 energy channels, 63% originated with a primary producer, 20% with detritus, and 17% with consumers; many of which could be traced back to detritus if the description were complete.

Food webs vary in the extent to which detritus derives from allochthonous or autochthonous sources and the particular form in which detritus occurs. Nonetheless, the linkages between detritus and grazer pathways are many and varied (Moore *et al.* 1988; Polis & Hurd 1996; Polis *et al.* 1997; Azam 1998), but often occur within two trophic levels from either source (Table 1). Food webs exhibit a high degree of inter- and intraguild predation and omnivory across the pathways, to the point that significant amounts of the biomass of intermediate and top predators can be traced back energetically to detritus (Table 2). The strength of these connections varies among and within ecosystems. For example, in oceanic islands top predators such as spiders and lizards link the two pathways, while in many reservoirs the pathways are strongly linked by a single species of fish. The 'microbial loop' in pelagic ecosystems (Fenchel 1988; Azam 1998) the amount of energy flowing from bacteria to metazoan zooplankton (and then fish) is substantial (Stockner & Porter 1988) while in others energy flow via this pathway is relatively small compared with energy flowing from primary producers to metazoan zooplankton (Cole *et al.* 2000).

The amount of energy flowing through the detrital pathway can equal or exceed that of the grazing branch (Hairston & Hairston 1993; Wetzel 1995; Cole *et al.* 2000; Cole & Caraco 2001; Heymans *et al.* 2002; Mulholland *et al.* 2002). Some food webs, such as those in caves, small streams in forested watersheds, and below-ground are based almost entirely on detritus (Hunt *et al.* 1987; Wallace *et al.* 1997; Jesser 1998). For other food webs the detritus pathway can have strong influences on the structure and dynamics of the grazer pathway by providing energy that can sustain higher densities of consumers than would otherwise be maintained if these consumers fed exclusively

Table 1 The percentages of trophic species that occupy the >2 trophic level (TL) and the top trophic level (TL) that obtain energy from detritus

Food web	% TL >2	% Top TL	Reference
NE US Marine Shelf	97.73	100	Opitz (1996)
Caribbean Reef	97.01	100	Link (2002)
Chesapeake Bay	100	100	Baird & Ulanowicz (1989)
St Marks Estuary	100	100	Christian & Luczkovich (1999)
Little Rock Lake	96.97	100	Martinez (1991)
Stony Stream	100	100	Townsend et al. (1998)
Canton Creek	100	100	Townsend et al. (1998)
St Martin Island	96	100	Goldwasser & Roughgarden (1993)
Ythan (w/parasites)	100	100	Huxham et al. (1996)
Coachella Valley Desert	100	100	Polis (1991)
Shortgrass Steppe Soil	100	100	Hunt et al. (1987)
Toolik Lake Tundra Soil	100	100	Doles (2000)
Lovinkhoeve Farm Soil	100	100	de Ruiter et al. (1995)
Horseshoe Bend Farm Soil	100	100	Hendrix et al. (1986)
Kjettslinge Farm Soil	100	100	Andrén et al. (1990)

Estimates are based on linkages provided in the descriptions of the webs (see references).

Table 2 Percentage membership of functional groups in the detritus (bacterial and fungal) and primary producer (root) energy channels of the soil food webs of the shortgrass steppe LTER site in northeastern Colorado, USA (Hunt et al. 1987), and the Lovinkhoeve Experimental Farm, Markinesse, The Netherlands (de Ruiter et al. 1995)

	Shortgrass steppe LTER site			Lovinkhoeve experimental farm		
	Energy channels			Energy channels		
	Detritus		1° Producer	Detritus		1° Producer
Functional group	Bacteria	Fungi	Root	Bacteria	Fungi	Root
Protozoa						
Flagellates	100	0	0	100	0	0
Amoebae	100	0	0	100	0	0
Ciliates	100	0	0	100	0	0
Nematodes						
Phytophagous Nematodes	0	0	100	0	0	0
Mycophaogous Nematodes	0	90	10	0	100	0
Omnivores Nematodes	100	0	0	100	0	0
Bacteriophagous Nematodes	100	0	0	100	0	0
Predatory Nematodes	68.67	3.50	27.83	89.1	10.6	0.4
Microarthropods						
Collembola	0	90	10	0	100	0
Cryptostigmata	0	90	10	0	100	0
Mycophagous Prostigmata	0	90	10	0	100	0
Nematophagous Mites	66.70	3.78	29.52	53.9	13.9	32.3
Predatory Collembola	– Not in description –			16.2	24.7	59.2
Predatory Mites	39.54	38.56	21.91	22.0	64.9	13.1
Annelids				Detritus	Bacteria	Fungi
Enchytraeids	– Not in description –			52.1	47.4	0.4

The estimates are based on nitrogen and carbon fluxes using biomass estimates from field samples and the model developed by Hunt et al. (1987).

on energy derived from the grazer pathway (Polis et al. 1997; Moore et al. 2003). For example, detrital inputs result in increased biomass of spiders and lizards on oceanic islands; high predator biomass can then lead to suppression of herbivores, with subsequent effects on plant abundance and species composition (Polis & Hurd 1996). In this case, both

the average lengths of the food chains and a 'trophic cascade' from predators to plants are driven by detrital inputs from outside the island ecosystem. Similarly, in reservoirs in the Midwestern USA, detritivorous fish (gizzard shad) attain high biomass via consumption of allochthonous and autochthonous detritus and excrete nutrients that can stimulate phytoplankton biomass (Schaus & Vanni 2000; Vanni 2002).

There are numerous variations of this phenomenon, to the point that primary producers rely on mineralized detritus for limiting nutrients (Coleman *et al.* 1983; Clarholm 1985; Ingham *et al.* 1985; Setälä & Huhta 1991). Yet, despite the empirical evidence presented in these examples, many basic treatments of food webs, such as in general ecology textbooks, grazer and detritus pathways are often treated separately, or when depicted together they are not connected in a significant way.

AN INTEGRATIVE FRAMEWORK FOR DETRITUS

We have highlighted the importance of detritus within communities and interconnectedness of the grazer and detritus pathways. It is clear that both population-level and system-level functions, even those far removed from the direct influences of detritus via food or habitat, are ultimately linked to its quality and quantity. Despite an understanding of such interconnectedness, detritus has been largely treated as a static and homogeneous resource (Odum 1963; Wetzel 1995). To integrate detritus fully into our understanding of factors driving the function and diversity of organisms, populations, and ecosystems, ecologists need to recognize the intimate links between detritus and other components of living systems, as well as, the heterogeneity and ontogeny of detrital resources.

Our concept of ontogeny (Fig. 2) encapsulates both the heterogeneous nature of detritus that is inherent in its constant state of flux and change that results from variation in sources, and the changes it undergoes during decomposition. Ontogeny includes the broad changes in particle size and chemical composition, which affects its overall lability as outlined by Swift *et al.* (1979), as well as the more subtle process like the immediate uptake of highly labile materials by consumers to minimal changes in recalcitrant materials that may be of more importance structurally than as food. The concept incorporates the association of detritus with minerals and other non-detrital material, which in turn, affects the physical availability of detritus to organisms. It explicitly presents detritus as a resource in food webs, a habitat for organisms, and the currency (e.g. energy, matter, nutrients) used in food web models incorporating detritus. The heterogeneity of detritus as depicted through ontogeny offers a sound basis to discuss and explore biodiversity, food web stability, biogeochemical cycling, organic matter accumulation, nutrient retention, energy flow, redox chan-
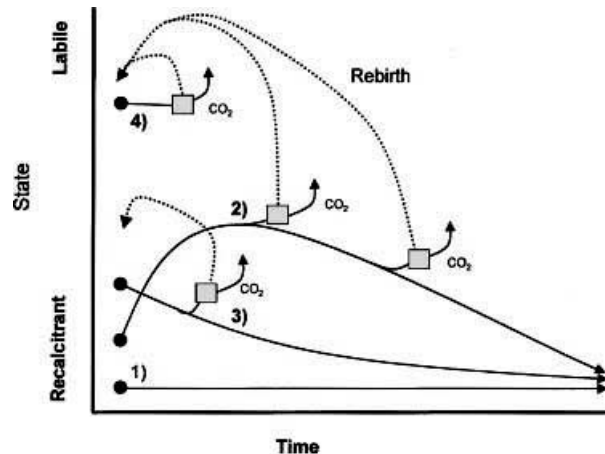

Figure 2 The ontogeny of detritus from creation (the death of organic material) to breakdown. Detritus enters systems in a variety of forms and qualities. Entry points can be represented by individual parcels or as complex detrital materials (e.g. whole organisms). As ontogeny proceeds (solid lines), diversity of materials is reduced, as more labile constituents are consumed and recalcitrant constituents or humic substances remain. The boxes represent the forms of material moving along the trajectories at a specific point in time. As the organic material is processed, it is mineralized (CO_2) and some labile fractions (dashed lines) may re-enter the pool (e.g. the breakdown of cell walls resulting the release of more labile cytoplasm and lipids) and initiate new trajectories. Trajectories 1–4 illustrate four general ontogenetic trajectories for different portions of detritus. (1) recalcitrant materials, such as lignins, that are minimally processed as they move from creation to humic substances; (2) chemically and structurally complex components of detritus (e.g. major portions of leaves and animals) for which physical processing results in an increase in overall lability before the most labile materials are scavenged, utilized, and respired leaving humic substances; (3) lower molecular weight material that becomes progressively more recalcitrant through extra-cellular biological and physical reworking (condensation and polymerization) until it forms humic substances; and (4) highly labile material, typically monomeric, that is rapidly scavenged, utilized and respired.

ges and habitat architecture under natural conditions or disturbed circumstances with a common currency.

Operational expressions of the heterogeneity and ontogeny of detritus are needed for modelling. Variation in particle size and/or chemical composition (e.g. C : N, lignin : N) may be useful for expressing detrital heterogeneity, which ranges from labile to recalcitrant forms, while changes in particle size and composition reflect inherent changes in detrital quality and colonization by organisms (Fig. 2). Microbes act upon a wide range of particle sizes, but may degrade smaller particles more rapidly owing to increased surface to volume ratio and access for cells and extra-cellular enzymes. In streams, shredders break down

larger pieces of debris, mainly via mechanic means, while collectors typically feed on much smaller particles, often via filter feeding (Wotton 1994; Wallace *et al*. 1999; Finlay *et al.* 2002). The existence of such interdependent processing chains is a fundamental feature of detritus-based food webs (Heard 1994a,b, 1995), and models of soil organic matter (Parton *et al.* 1983).

The ontogenetic shifts we describe show considerable interdependence among carbon sources, microbial decomposers, and detritivores within detritus pathways. Thus, models including detritus need to make explicit the components of detritus pathways that are considered. The close physical association between microorganisms and particulate detritus can make it difficult to operationally separate detritus from the microbial assemblage and detritivores that it supports. For example, we currently have few tools allowing for the separation of microbial and detrital carbon or to trace their contribution to consumers (but see Hall & Meyer 1998). However, the quality of detritus is tied to the degree of microbial colonization such that it may be more useful in some cases to consider them as grouped entities as higher consumers in the detrital branch may not distinguish between the consumption of detritus and the microorganisms that feed on it. These distinctions raise interesting challenges for how detritus should be treated in community models, running from a coarse aggregation of all detritus and its associated consumers as a single community module, to a more finely resolved approach that would keep track of the different 'taxa' (categorizations based on size, lability, chemical qualities) of detritus, and microbial and detritivore diversity.

FOOD WEB AND ECOSYSTEM IMPLICATIONS

Viewing detritus as an integral dynamic resource of ecological systems rather than a static independent resource has important implications for the interpretation of many classic ecological theories based solely on energy directly arising from primary productivity. We have already addressed the extent to which organisms throughout food webs of systems are supported by detritus or primary producers (Moore & Hunt 1988; Polis & Hurd 1996; Wallace *et al.* 1997; Bouillon *et al.* 2000; Chanton & Lewis 2002; Finlay *et al.* 2002; McCutchan & Lewis 2002). In this section we discuss how detritus might affect the dynamics and stability of food webs, trophic height or food chain length, the distribution of biomass among trophic levels, a trophic cascade, and biodiversity.

Dynamics and stability

The non-living nature of detritus influences the structure and dynamics of the living species that depend on it as an energy source in three important ways. Unlike living organisms, detritus neither reproduces, nor directly affects the input of new material. This density independence in the accrual rate of detritus exemplifies a quintessential donor controlled process (*sensu* Pimm 1982). Secondly, its ontogeny is dependent in part on the actions of other species, in that, when consumed detritus undergoes transformations (i.e. ontogeny per Fig. 2) as it decomposes from one form to another. Finally, detritus does not require energy for maintenance, hence has the capacity to serve as reservoirs of energy or supplement the energy needs of consumers that have been traditionally viewed to rely only on living organisms for energy.

The input rates of detritus and the detrital pool size have been shown to affect the dynamic stability (resilience) of food web models that incorporated two of the three unique features of detritus (De Angelis *et al.* 1989; Moore *et al.* 1993). Before we integrate detritus into a system with producers, we will first consider separately the familiar primary-producer based Lotka-Volterra representations of food chains and their detritus-based analogues (Moore *et al.* 1993). For the primary-producer food chain, let:

$$\frac{dP}{dt} = r_p P - s_p P^2 - c_{hp} PH \tag{1a}$$

$$\frac{dH}{dt} = -d_h H + e_{hp} a_{hp} c_{hp} PH \tag{1b}$$

where P and H represent the biomasses (g C m^{-2}) of plants and herbivore respectively, r_p is the intrinsic rate of increase of the plant (year^{-1}), d_h is the specific death rate of the herbivores (year^{-1}), s_p and c_{hp} are the intra-specific coefficient for the plants and consumption coefficient of the herbivores [(g C m^{-2})$^{-1}$ year^{-1}] respectively, and a_{hp} and e_{hp} are the assimilation and production efficiencies (%).

For the detritus-based analogues of the primary producer-based equations let:

$$\frac{dD}{dt} = d_m M - a_{md} c_{md} MD + R \tag{2a}$$

$$\frac{dM}{dt} = e_{md} a_{md} c_{md} MD - d_m M \tag{2b}$$

where, D and M are the biomass of detritus and microbes, respectively, d_m the density independent mortality rate of microbes, a_{md} the assimilation rate of detrital biomass by microbes, c_{md}, the consumption rate of detrital biomass by microbes, e_{md}, the conversion efficiency of detrital biomass to microbial biomass and R, the allochthonous supply of detrital biomass to the system.

If we compare the levels of input required for the primary producer and detritus based food chains to be energetically feasible (*sensu* Roberts 1974) where the steady-state values for all species are greater than zero ($X_i^* > 0$ for all i species),

we see that the detritus-based food chains are feasible at lower levels of input than their primary producer counterparts, as there are no maintenance or losses due to intra-specific competition.

$$M* = Re_{md}/(d_m - d_m p_{md}) \qquad (3a)$$

$$P* = (r_p a_{hp} e_{hp} c_{hp} - s_p d_h)/a_{hp} e_{hp} c_{hp} \qquad (3b)$$

The two-species detritus-based food chain is globally asymptotically stable (Neutel *et al.* 1995). While the same is true for the similarly structure primary producer analogue (May 1973), the two differ in an interesting and important way. The diagonal term of the Jacobian matrix for system of equations of the detritus and microbe food chain is negative, a necessary (but not sufficient) condition for matrix stability:

$$\alpha_{dd} = -a_{bd} c_{bd} M \qquad (4)$$

The stabilizing effect of detritus on this system is achieved not through self-limitation of the resource (as in classic primary-producer models) but rather as a result of the constant inputs of detritus (R).

The results of Neutel *et al.* (1995) when coupled with those of (Moore *et al.* 1993) positions detritus as a more stable, persistent reservoir of energy, than primary producers alone over a wide gradient of productivity (Fig. 3). Monte Carlo comparisons of models based on detritus like the one described above to traditional depictions based on primary producers yielded qualitatively similar results over a range of parameter values (Moore *et al.* 1993; Moore & de Ruiter 2000), but were more likely to support energetically feasible food chains (*sensu* Roberts 1974) and were more resilient (faster return-times *sensu* Pimm 1982).

Spatial and temporal scaling

An underlying tenet of spatial modelling is that the spatial average of the system poorly describes overall system dynamics given the variability of the 'local spatial environment' experienced by the different species (Durrett & Levin 1994). The inclusion of detritus into spatial food web theory offers interesting challenges given the donor-controlled nature of its dynamics and the linkages that detritus food chains have with grazer-based food chains. Detritus is an energy source that, through its diverse structural qualities, has a residence time that spans seconds to millennia. Models that include allochthonous and autochthonous inputs of detritus (Moore *et al.* 1993; Polis *et al.* 1997; Huxel & McCann 1998), which typically have only included space implicitly, show that detritus can have important stabilizing influences and affect the trophic dynamics. While, these models are part of a more general framework that explores the importance of weak interactions as stabilizing influences (McCann *et al.* 1998; Post
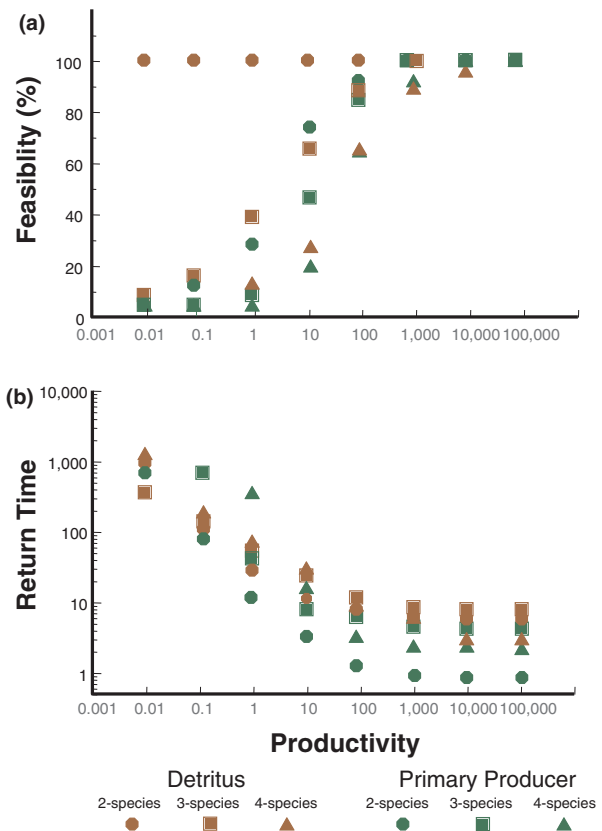

Figure 3 The effect of productivity on the feasibility and resilience of primary producer-based (green) and detritus-based (brown) food chains of length 2 (●), 3 (■), and 4 (▲) using eqns 1 and 2 and the parameterizations as presented in Moore *et al.* (1993). Feasibility is the percentage of food chains at a given level of productivity where all species maintained positive densities at equilibrium (Roberts 1974). The resilience is expressed as the return time (RT), estimated as RT $= -1/\text{real}(\lambda_{max})$ were real (λ_{max}) is the real part of the dominant eigenvalues. Depending on the assumptions used to establish the death rates and the consumption coefficients, productivity scales between 4 and 36 g C m^{-2} year^{-1}.

et al. 2000) other models have explicitly included the interplay between population dynamics and material cycling (DeAngelis 1992; Loreau 1994, 1995, 1996, 1998).

Although initial attempts to model the effects of detritus on the dynamics and functioning of communities and ecosystems ignore space, further progress will depend on explicit considerations of space and scale (Levin 1992; Pascual 1993). The movement of detritus between habitats is an essential to dynamics, and is implicit in the models with fixed levels of detrital input, which mimic input from outside the local system. Use of stochastic spatial models and individual based models (Durrett & Levin 1994; Dieckmann *et al.* 1999; Pascual *et al.* 2002) to explore the dynamic consequences of detritus is also likely to provide new and important insights.

The quality and quantity of detritus varies among systems, with the different forms of detritus being transported at different rates and across different spatial scales. The following two scenarios illustrate the importance of scaling, and the movement of detritus. Callaway & Hastings (2002) studied the importance of the spatial distribution of detritus and primary producers and the movement of species occupying different trophic levels. Focusing on two patches, with allochthonous inputs of detritus subsidizing one patch in a donor-controlled manner, an immobile resource species (e.g. plants) forming the second patch, and consumers that moved randomly between the two patches with the capability of consuming the detritus and the resource species. In contrast to the single patch case involving only the immobile resource species, the resource population can increase both in the subsidized patch and in the overall system. This kind of result should emerge when the spatial distribution of detritus and the spatial scales of movement of species are very different.

The second scenario illustrates that similar issues arise when considering temporal variability. In this case consumers reside in a single patch but receive primary production and detritus at a variable rate from within the patch, as well as constant inputs of detritus from outside the patch. This scenario was highlighted in the systems of Baja California islands investigated by Polis and colleagues (Polis & Hurd 1996; Polis *et al.* 1997; Stapp *et al.* 1999), where the allochthonous input is relatively constant, while the level of primary productivity varies tremendously among years, depending on precipitation. Consequently, the allochthonous input greatly changes system dynamics by maintaining a base level of consumers that can respond to temporal pulses of productivity. The level of temporal variability of detrital input is low relative to the time scale over which primary productivity varies. The presence of a low steady input of energy, greatly affects the dynamics of a system in the presence of another large but temporally variable input of energy.

Food chain length

We have emphasized that significant amounts of consumer and predator biomass could be traced back to detritus, and implied that this added production supports longer food chains that would be in its absence. However, while theoretically tractable, very little empirical evidence supports the notion of food chains being limited in length for energetic reasons (Oksanen *et al.* 1981; Pimm 1982; Moore & de Ruiter 2000; Post *et al.* 2000). We propose that part of the reason for the lack of evidence has been the reliance on net primary productivity alone and the affinity that small ectotherms have for detritus compared with large endotherms.

An illustration of these points can be seen when investigating the energetic costs or feasibility of maintaining a food chain of a given length. Detritus-based and producer-based models both suggest that energy supply limits the length of food chains (Fig. 3). However, the amount of dead organic matter needed to support bacteria and fungi, if not larger detritivores, is lower on average than what would be required to support physiological and morphologically comparable herbivores. Moreover, the resident time of energy within detrital systems is longer owing to the absence of death and the internal cycling in detritus-based systems enhances the efficiency of detrital vs. grazer-dominated food webs. This detritus-based energy supports species at higher trophic levels, and supports longer food chains and greater food web complexity in unproductive systems (Moore & Hunt 1988; Hairston & Hairston 1993; Kaunzinger & Morin 1998).

Comparisons of primary producer-based and detritus-based food chains from within published food webs reveal that they possess similar structural properties (Moore & Hunt 1988), anomalies in the descriptions notwithstanding (Briand & Cohen 1989; Moore *et al.* 1989). An interesting pattern immerges when the physiologies of the organisms are taken into consideration (Phillipson 1981). Detritus is fed upon largely by ectotherms (unicellular and multicellular), while primary producers are feed upon by both ectotherms and endotherms. There are clear differences in body sizes, life spans, and energetic efficiencies between these physiological groupings, and inextricable links to these life history and morphological characteristics, the form and rate of energy input (detritus or primary productivity), and dynamic stability of the food chain. Consider models of primary producer-based and detritus-based food chains of the forms presented by Moore *et al.* (1993), whose parameters have been set to represent organisms that possess growth rates, death rates and energetic efficiencies that are either ectotherm-like or endotherm-like. The feasibility (*sensu* Roberts 1974) and resilience (*sensu* Pimm 1982) of these models confirm the earlier findings that detritus-based food chains are more feasible and resilient than there primary-producer indicate, but further indicate that detritus-based systems favour ectotherm-like organisms over endotherm-like organisms (Fig. 4).

Trophic Cascades

Hutchinson (1959) and Hairston *et al.* (1960) revealed how energetics and dynamics interact to influence community structure. The amount of available energy after each predator–prey interaction diminishes and limits both diversity and trophic structure, and the trophic structure influences the placement of available energy in a community. Consumers regulate the density and dynamics of prey, creating a cascade of regulation and biomass. There is strong empirical evidence
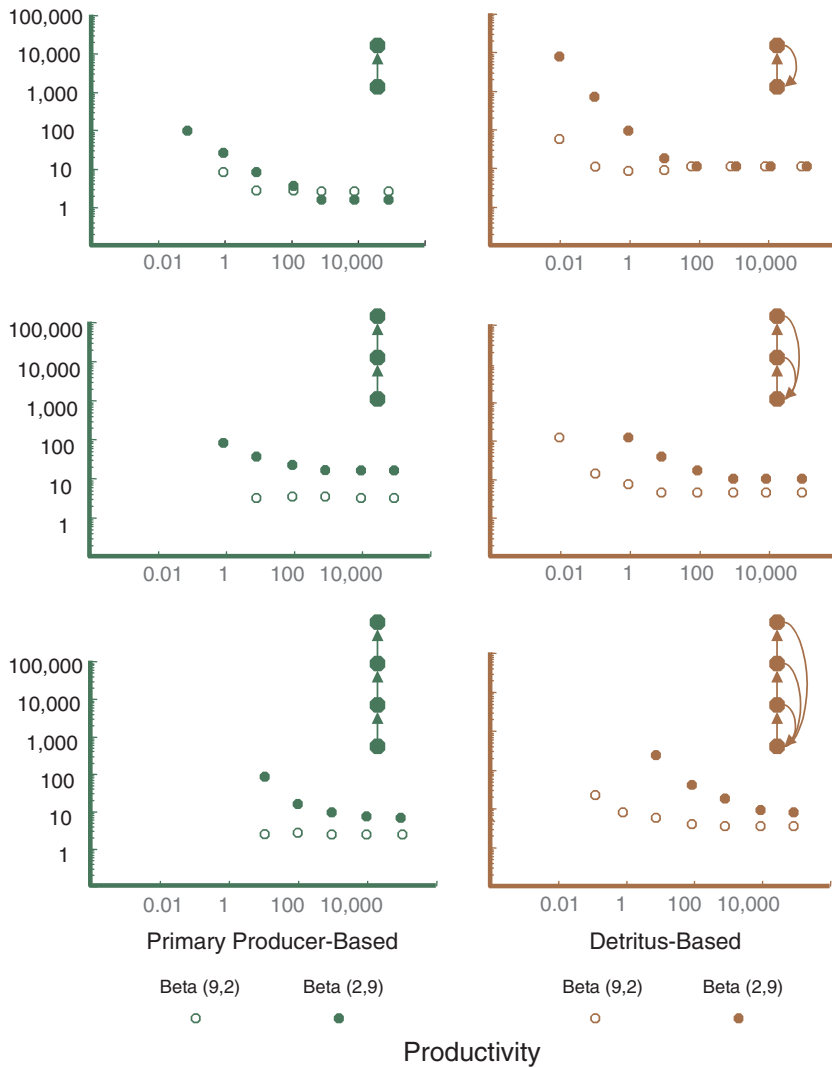
Figure 4 The resilience, as measured by return-time (RT), of primary producer-based (green) and detritus-based (brown) food chains of length 2 (●), 3 (■), and 4 (▲) using eqns 1 and 2 parameterized for ectothermic (open symbols) and endothermic species (closed symbols). The ranges of parameters selected were similar to those used in Fig. 3, but the selections for ectotherms followed a Beta (9, 2) and the selections of the endotherms followed a Beta (2, 9) (redrawn from Moore & de Ruiter 2000).

in support of trophic cascades for aquatic systems (Carpenter *et al.* 1985; Carpenter & Kitchell 1988; Powers 1990) and less support for the terrestrial literature (Strong 1992; Shurin *et al.* 2000; Preisser 2003). The underlying assumption of the traditional cascade model was that primary producers provided energy to the base of a food chain, and that structure developed in the manner proposed by Hutchinson (1959). If biomass accumulated at the upper trophic level, the top predators would consume and decrease the biomass of their prey, thereby releasing predation pressure on the prey of the prey allowing for them to increase, and so on (Oksanen *et al.* 1981). It becomes clear with a little algebra that the accumulation of biomass at the upper trophic levels, a trophic structure associated with a cascade, occurs at relatively high rates of energy input, higher still than the rates required to maintain an additional trophic level. The models further indicate that at these levels of productivity, the structures are

prone to oscillations and instability (Rosenzweig 1995; Moore & de Ruiter 2000; Neutel *et al.* 2002).

Work in the past decade more clearly focused on detritus, has added a different dimension to the debate on trophic cascades (Polis & Strong 1996). Closer examination of the food webs that were purported to have followed the cascade model revealed that consumers at the upper trophic levels were in fact were omnivorous by obtaining energy not only from the level immediately below it but from several trophic levels, and more importantly, obtained energy from detritus, leading to the concept of an apparent trophic cascade. In this case, the energy from detritus not only supported the upper trophic level, but fuelled the predation pressure that it exerted on its prey as well.

We present a model of the apparent cascade that offers a stable alternative to the traditional cascade model. The traditional cascade model would assume that energy passes

through a primary-producer-based food chain to a top predators, and as noted above is prone to oscillations and instability. The apparent cascade model assumes that the top predator obtains energy from two pathways. Assume that the first level includes a pool of resources that supports two parallel food chains linked together by a top predator in the manner presented by Post *et al.* (2000). The parallel food chains could be detritus-based and primary producer-based much like the scenarios presented by Polis & Hurd (1996) or modelled like Callaway & Hastings (2002). Finally, assume that the pathways leading to the top predators differ in terms of the physiologies of their respective organisms and the rates that they turnover. Comparisons of the two models when structure and parameterized along the lines of McCann *et al.* (1998) indicate that the model of the apparent cascade is more stable than the model of the traditional cascade model, for the same overall input of energy (Fig. 5). The linked pathways were most stable and less prone to oscillation when the top predators received from 20 to 60% of their energy from either pathway, rather than 100% from a single pathway.

Biodiversity and detritus

The links between detritus and biodiversity are reciprocal in nature, particularly when viewed from our perspective of ontogeny. The physical and chemical diversity of substrates entering detrital food webs sets the ecological stage for the evolution and maintenance of detritivore diversity. In turn, the diversity of detritivores impact nutrient cycling rates and ultimately feed back to accentuate producer and consumer diversity (Moore *et al.* 2003). In addition, the strength and direction of links between detritus and biodiversity are dynamic. After death or excretion, organic compounds embark on a chemical and physical succession that generates a mosaic of resources (carbon, energy and nutrients) and conditions (habitats and environments) for producers and consumers. Associated with these shifts in forms and composition of detritus during its ontogeny are associated changes in the composition and functioning of biological communities. Many questions concerning detritus and diversity are only recently beginning to be addressed. These include: (1) What are factors that determine species richness in detrital communities? (2) How does the diversity of detritivores affect key rates and fate of detritus processing and ultimately feedback to producer productivity and ecosystem diversity? and, (3) How does species diversity of organisms associated with detritus differ at different stages of its ontogeny? Recent work illustrates the interdependence and feedbacks between diversity of detritus and its consumers.

The diversity and abundances of microbial populations is related to both the diversity and quality of detritus
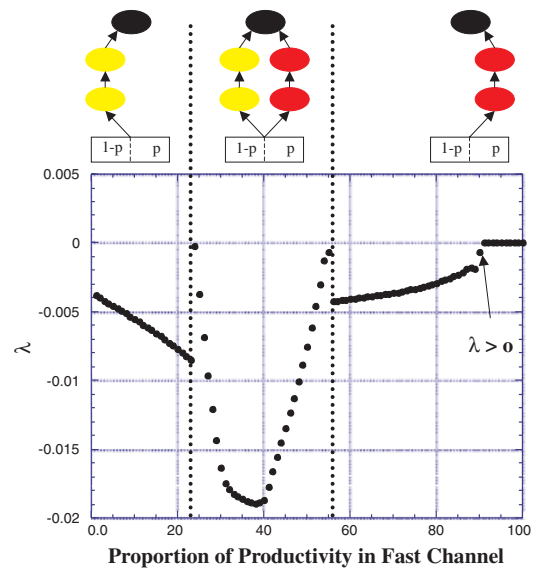

Figure 5 The dominant eigenvalues for a series of apparent cascade models along a gradient of resource allocation. The model includes two parallel food chains (red and yellow) drawing energy from a heterogeneous source and linked by a common predator (black). The food chains differ in the rates in which that process and turnover energy, i.e. fast (red) and slow (yellow) pathways. The *x*-axis represents the proportion of resource passing through the fast channel (p), while the *y*-axis represents the dominant eigenvalue (λ) for the system at each iteration of partitioning of resource. The total amount of energy passing through each system is the same for each iteration. The dashed vertical lines represent monentary unstable transitions where one of the pathways accumulates more biomass at upper levels than at the lower levels. Note that the most stable configuration occurs when the two pathways are coupled, and unstable if most of the energy passes through the fast pathway ($\lambda > 0$).

substrates. We have known for some time that change in substrate quality can affect the relative abundance bacteria and fungi, where materials of high C : N ratios (>30 : 1) favour colonization by fungi, while more labile materials with low C : N ratios (<30 : 1) favour bacteria, and that with these changes come shifts in the abundances of the consumers of bacterial and fungi (Hendrix *et al.* 1986; Moore & Hunt 1988; Andrén *et al.* 1990). Analyses of microbial products such as DNA, phospholipids fatty acids (PLFA), and glomalin have been correlated with the microbial diversity and the diversity of substrates and plants (Butler *et al.* 2003). Many ecologists are now using molecular techniques that distinguish sequence variation in the 16S rRNA genes to infer phylogenetic relations and diversity of whole communities (Chelius & Moore 2004; Dilly *et al.* 2004; Kang & Mills 2004). This approach has revealed that bacterial and archaeal diversity may develop in parallel with plant communities, with changes in plant species and their

substrates influences the diversity of bacteria (Kang & Mills 2004). As the diversity of substrates, and in particularly the range in the quality of substrates increases, the array of enzymes needed to break the more recalcitrant bonds increases significantly, resulting in higher overall microbial diversity.

The biodiversity of detritivores and decomposers is affected by both the quantity and type of detritus (Lake *et al.* 2000; Palmer *et al.* 2000). In terrestrial systems the densities and diversity of protozoa and invertebrates follow the broad changes in the quantity and quality of detritus. Studies of published webs have found significant correlations between the diversity of resources (primary producers and detritus) and the diversity of consumers and predators (Moore & Hunt 1988; Yodzis 1988). Manipulative field studies have provided compelling evidence as well. For example, litter exclusion greatly reduced the biomass of stream invertebrates, while several invertebrate species, including shredders, collectors and predators, disappeared altogether (Wallace *et al.* 1997), while increased deposition of detritus as dead phytoplankton increase resources for, and hence diversity of, detrital consumers in sediments (Palmer *et al.* 2000).

The diversity of decomposers and detritivores affects the quantity and quality of detritus throughout decomposition. Laboratory and field studies suggest that the species richness of detritivores can increase the rate at which leaf matter is broken down in streams (Jonsson & Malmqvist 2000; Jonsson *et al.* 2001a,b). In addition, the species of detritivore (which species is present) affects detrital processing rates in streams (Pringle *et al.* 1999; Crowl *et al.* 2001; March *et al.* 2001) and decomposition processes in grasslands (Cragg & Bardgett 2001). Specifically, the diversity of detritivores results in non-additive changes in particle capture and consumption of detritus, and thus efficiency of energy conversion (Cardinale & Palmer 2002). In contrast to these studies on streams, which suggest little redundancy among species in their effects on ecosystem processes, studies marine sediments and soils suggests that there is considerable redundancy among detritus consumers (Andrén *et al.* 1995, 1999; Levin *et al.* 2001).

A GENERAL MODEL OF DETRITAL DYNAMICS

As an illustration of the importance of the integrative framework for detritus, we present the simplest model incorporating detrital ontogeny and decomposer diversity. The model contains a recalcitrant detrital pool (R), a labile detrital pool (L), a bacterial population (B), feeding on L, and a fungal population (F) feeding on both detrital pools. Consider the following energetic model (also depicted in Fig. 6):
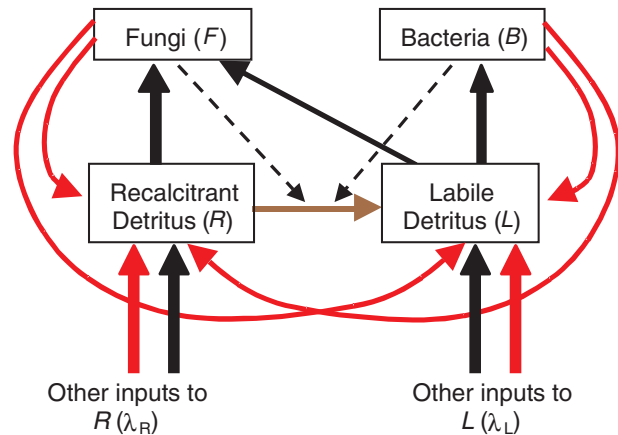

Figure 6 Schematic of the general ontogeny model. As in Fig. 1, black arrows represent flow of detritus derived energy and red arrows represent creation of new detritus from external and internal sources. The brown arrows represent ontogenetic change of detritus.

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \lambda_R + \varepsilon d_F F + \delta d_B B - pR(1+\alpha F) - (1-a_{RF})C_{RF}RF$$

$$\frac{\mathrm{d}L}{\mathrm{d}t} = \lambda_L + (1-\varepsilon)d_F F + (1-\delta)d_B B + pR(1+\alpha F)$$
$$- (1-a_{LF}c_{LF}LF) - (1-a_{LB})c_{LB}LB$$

$$\frac{\mathrm{d}F}{\mathrm{d}t} = e_{RF}a_{RF}c_{RF}RF + e_{LF}a_{LF}c_{LF}LF - s_F FF - d_F F$$

$$\frac{\mathrm{d}B}{\mathrm{d}t} = e_{LB}a_{LB}c_{RF}LB - s_B BB - d_B B$$

$$(5)$$

The model possesses five pathways of energy flow: (1) the flow of material from the recalcitrant to the labile pools due to abiotic factors such as weathering and leaching (governed by the rate constant p), (2) the flow from R to L facilitated by extra-cellular enzymatic degradation by fungi (rate constant $p\alpha$), (3) the consumption of recalcitrant material, only by fungi (a_{RF}), and (4 and 5) the consumption of labile material by both fungi (c_{LF}) and bacteria (c_{LB}), a_{RF}, a_{LF} and a_{LB} are the assimilation efficiencies, and $_{RF}$, e_{LF} and e_{LB} are the conversion yield efficiencies corresponding to each consumption pathway. The model also takes into account the input from external sources to the recalcitrant and labile detritus pools (λ_R and λ_L, respectively), inputs from the fungal population to each of these pools (at per unit biomass rates εd_F and $(1 - \varepsilon)$ d_F, respectively) and inputs from the bacterial population [at per unit biomass rates δd_B and $(1 - \delta)$ d_F]. Lastly, fungal and bacterial death is governed by the rate parameters d_F and d_B, and intraspecific competition s_F and s_B, respectively.

As with any model a few words of caution are in order. First, a more realistic way to integrate detrital ontogeny into

food web models would allow the state of detritus to take on a continuous range of values corresponding to different amounts of lability, and might build upon ideas from structured population modelling (Metz & Diekman 1986). Second, we explored the models behaviour by varying the consumption of labile material by fungi (c_{LF}), the transfer rates from one pool of detritus to another (α), and the amount of recalcitrant material (λ_R) entering the system. Clearly the model is sensitive to changes in other parameters, for example, changes in the assimilation and production efficiencies of the microbes to reflect changes in the quality of detritus. However, a model and analysis of such depth is beyond the scope of this paper.

Figure 7 illustrates that fungal and bacterial coexistence at equilibrium is possible in this model, and that coexistence is

accompanied by a range of dynamic states, from equilibrium to what appears to be a stable limit cycle (Fig. 7a). Coexistence of fungi and bacteria is more likely to occur within a window of parameter space where the fungal death rate exceeds the bacterial death rate, the bacterial assimilation efficiency exceeds that of fungi, or the bacterial labile detritus consumption rate exceeds that of the fungi.

This simple model reveals how the ontogeny of detritus influences species diversity (Fig. 7b and c). Consider for example the equilibrium behaviour of this model, depicted as a function of the rate of transfer from the recalcitrant pool to the labile. At low rates of fungi mediated transfer of detritus (α), fungi are favoured over bacteria, to a point where only fungi are present, because the labile pool is too small to support bacteria (Fig. 7b). However, as α increases,
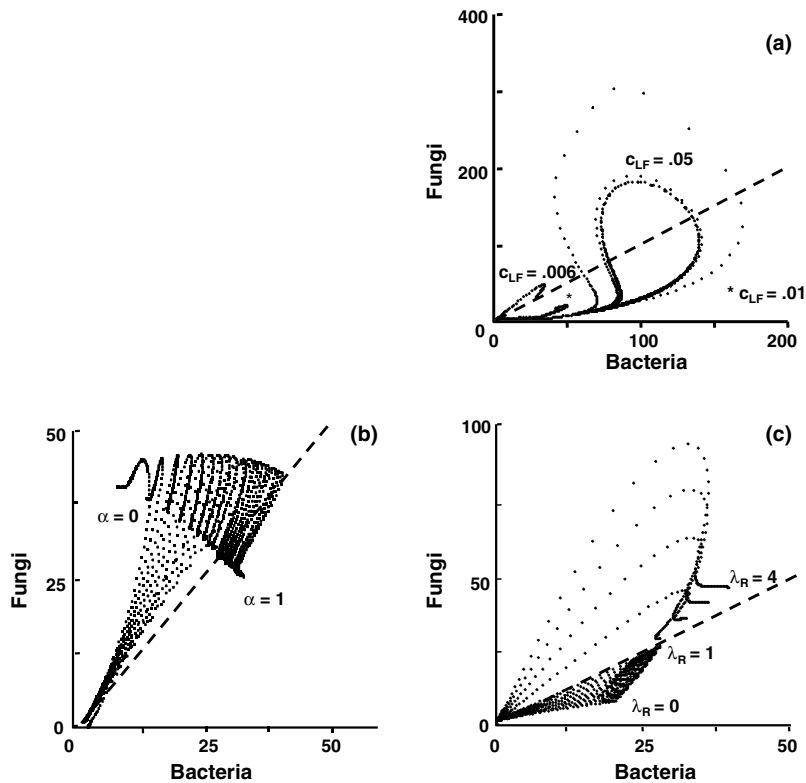

Figure 7 Detrital ontogeny, some of which is mediated by agents in the food web, can lead to stable coexistence of species. Each graph depicts a series of steady state behaviours through the phase space of bacteria and fungi beginning with and then varying the parameters listed below. The parameters listed below result in a steady state where fungal biomass equals bacterial biomass (the dashed lines represent the isoclines where fungal biomass equals bacterial biomass). (a) The model exhibits a range of dynamic states. Increasing the feeding rate of bacteria on the labile substrate (c_{LF}) moves the system from a stable equilibrium to a limit cycle ($c_{LF} = 0.006$, $c_{LF} = 0.01$, and $c_{LF} = 0.05$); (b) Increasing α, the parameter that governs fungi mediated transfer of material from the recalcitrant to the labile pool, causes the system to change from a fungi dominated one to a system dominated by bacteria (α varied from 0 to 1 at increments of 0.05); (c) Likewise, varying the input into the recalcitrant pool shifts the system between one dominated by fungi to one dominated (λ_R varied from 0 to 1 at increments of 0.1 and from 1 to 4 at increments of 1). Unless varied, the parameters used here are $d_F = 0.1$, $d_B = 0.1$, $s_F = 0.001$, $s_B = 0.001$, $P = 0.005$, $\varepsilon = 0.2$, $\delta = 0.2$, $c_{LB} = 0.006$, $c_{RF} = 0.001$, $c_{LF} = 0.005$ $e_{LB} = 0.8$, $e_{LF} = 0.8$, $e_{RF} = 0.8$, $a_{LB} = 0.9$, $a_{LF} = 0.9$, $a_{RF} = 0.9$, $l_R = 0.2$, $\lambda_L = 2.0$ and $\alpha = 0.5$.

it is possible for both populations to coexist, and for bacteria to overtake fungi. This result highlights both the harmony and dissonance between the two microbial populations: while they compete for resources, bacteria are also dependent on fungi to create labile material for consumption. There are many parallels to this phenomenon in other food web subcomponents. Coexistence of bacteria and fungi also depends on the amount of recalcitrant material (λ_R) entering the system; if inputs are dominated by labile material, λ_L (i.e. recalcitrant inputs are low), fungi cannot survive (Fig. 7c). However, increasing λ_R leads to coexistence (Fig. 7c), mirroring observations that inputs of labile material that are high relative to other inputs can generate a bacteria dominated microbial system (Hendrix *et al.* 1986; Andrén *et al.* 1990; Moore & de Ruiter 1991).

CONCLUSIONS

Ecologists have conducted numerous studies on the characterization, classification and transformations of detritus, but generally ignored detritus when examining fundamental questions of community organization. Beginning with the simple premises that detritus is a ubiquitous and integral component of communities and that few top predators derive their energy from either primary producers or detritus exclusively, we argue that the partitioning of communities into grazer and decomposers subsystems should move beyond its descriptive and heuristic value, and work its way into the basis of general ecological theory. We have emphasized how the impact of detritus is best understood if differences between the dynamics of detritus, the 'brown' part of the food web, and the dynamics of the 'green' part of the food web are recognized and reconciled. We conclude with a series of propositions and recommendations for future studies.

We propose that the impact of detritus is best understood through a focus on the ontogeny of detritus, the changes in detritus from the time of its creation until only completely recalcitrant material is left. Detritus goes through a series of changes through time, and these changes are both mediated by and have large effects upon the organisms that process the detritus. The transformations represent multiple entry points into system as the action of organisms on detritus during the aforementioned changes brings detritus-based energy into the community. The infusion of this energy into the community and its passage to top predators affects the diversity, structure and dynamic properties of the community. This will require that new techniques be developed so we can know what is actually consumed and assimilated when detritivores eat 'detritus', i.e. what fraction of the detrital pool, and the extent to which detritus vs. microbes are assimilated. Promising techniques include using stable isotopes and biomolecules that are specific to certain organisms as tracers. While we have provided a start to understanding the impact on diversity through simple box models, a deeper understanding of the role of ontogeny awaits more detailed models.

Experiments are needed that address the effects of detritus stoichiometry on food webs. The quantity of detritus and nutrients could be manipulated, and one could develop predictions about food web response based on C : N : P ratios. For example, microbes within the brown world could either be net recyclers or immobilizers of nutrients depending on the C : N : P ratio, and this could have variable effects on the rest of the food web including green world components. Reiners (1986) articulated the importance of this approach, DeAngelis (1992) provided an initial framework, while Sterner & Elser (2001) provide the most thorough treatment to date. The importance of stoichiometry is still being vetted, and detritus has yet to make its way into the mainstream of ecological theory and food webs.

Greater attention to temporal and spatial scaling of energy sources is needed. This is true for primary production as well as detritus. Differences in spatial and temporal scales of the distributions and input rates of resources, coupled with the unique attributes of detritus appears to be an important stabilizing feature of food web models, particularly when linking pathways originating from different resources to a common suite of predators. This simple observation needs to be amplified by considering the ontogeny of detritus, since the interaction between spatial and temporal scales will be important for determining the role of detritus. Similarly, cases where inputs of detritus act as integrators over longer time scales also will require approaches that are different than the typical instantaneous response in most theoretical formulations in ecology.

Finally, studies attempting to relate net primary productivity to species diversity and food chain length or the importance of trophic structure on production, i.e. bottom-up vs. top down controls, should incorporate detritus into the production side of the relationships. Estimating net primary production alone or thinking of the issues without taking into consideration detritus-based energy has yielded ambiguous results (Strong 1992; Rosenzweig 1995; Moore *et al.* 2003). We propose that a full accounting of detritus-based energy in terms of source, quantity, and quality will clarify our understanding of the role of energy input in structuring communities. Our treatment here suggests that the lower threshold of energy input required to support upper trophic levels may be far lower than current studies have explored, particularly when the unique properties of detritus and the physiologies and life histories of its dominant consumers are considered.

Nearly a half a century ago, G. Evelyn Hutchinson (1959) asked '…why are there so many kinds of animals'.

At that time ecology had split into two camps, one focusing on species interactions within the green-world pathway, the other on the flow of energy and matter through ecosystems with inclusion of the detritus and the brown-world pathway. Progress towards answering fundamental ecological questions of the distribution and abundance species can only be made by merging the green world of primary producers and the brown world of detritus in a new integrative ecology.

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