

# Primary community assembly on land – the missing stages: why are the heterotrophic organisms always there first?

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## Summary

**1** It is proposed that as a general rule primary community assembly by autotrophs is preceded by a previously unrecognized heterotrophic phase that may be instrumental in facilitating the establishment of green plants and consolidating the assembly process.

**2** This heterotrophic stage, of variable duration, involves the allochthonous input of both dead organic matter and living invertebrates sufficient to allow the initial establishment of functioning communities comprised of scavenging detritivores and predators.

**3** Evidence for deposition of such materials onto newly exposed land surfaces and the development of such animal communities is summarized for a variety of sites and substrates worldwide.

**4** It is suggested that these heterotrophic communities conserve nutrients, particularly nitrogen, and facilitate the establishment of green plants.

*Key-words:* allochthonous detritus, colonization, facilitation, invertebrates, succession

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## Introduction

Read any core ecology textbook regarding the initial stages of primary community assembly or succession and you will discover that this is essentially a process involving the colonization and establishment of vegetation on newly exposed substrates (Colinvaux 1993; Begon *et al.* 1996; Krebs 2001). Stand on one of these substrates devoid of green plants, such as a newly exposed glacial moraine, a shingle beach or a cooled volcanic lava flow or ash field and you will experience a different scene. The surface often teems with moving organisms that include active predators as well as detritivores. Heterotrophic protozoa and nematodes are often similarly abundant in the interstices of the mineral substrate. Are these communities not an integral part of community development? Have food webs not already established? How do these primary and secondary heterotrophic consumers survive in an environment apparently devoid of the autochthonous primary production required to support them? Why do the predators and scavengers always seem to be the first to arrive? Clearly there is a mismatch between

accepted wisdom and observed events surrounding the earliest stages of community assembly.

Here we wish to propose that as a general rule community assembly by autotrophs is preceded by a largely unrecognized heterotrophic phase that may be instrumental in facilitating the establishment of green plants and consolidating the process of community development. Our ideas evolved from a continuing long-term study of communities on proglacial terrain in the high Arctic (Hodkinson *et al.* 2001) and a consideration of data for equivalent primary ‘successions’ elsewhere.

Initial theories of primary succession were developed by plant ecologists (e.g. Clements 1907). Succession was viewed as an ordered, directional and deterministic process in which plant communities developed through a series of stages towards a climax vegetation type. An alternative theory, based on the ideas of Gleason (1939), which has gained wider acceptance more recently, is that ‘succession’ is a probabilistic process in which community development is driven by the availability of propagules and by competition between species. This does not suppose a fixed end point or climax, simply development towards a most mature vegetation type (Colinvaux 1993). Hence the phrase ‘community assembly’, which implies a less deterministic process, is tending to replace the older term succession. Young *et al.* (2001) explore the issues arising from these contrasting ideas.

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Successful biological colonization of inert substrates, either naturally occurring or man-made, requires a source of energy, nutrients, carbon and water, all of which may be initially absent (Griggs 1933; Davis 1986; Marrs & Bradshaw 1993; Miles & Walton 1993b; Frenot *et al.* 1995, 1998). Although colonizing photosynthetic organisms have the ability to fix carbon, a range of essential nutrients, nitrogen and phosphorus in particular, is a prerequisite for growth. These nutrients become available through physical weathering of the substrate over time, the activities of heterotrophic organisms breaking down available biological materials or, in the case of nitrogen, through fixation and precipitation in both soluble and particulate form. Organic matter accumulation is also important for the retention of the water and nutrients to support plant growth. Hidden in the literature is a significant body of information that suggests that aerial deposition of highly dispersive invertebrates and/or allochthonous detritus may provide the initial inputs of energy and nutrients that initiate the process of community assembly. Littoral deposition of detritus may also be important in particular coastline situations (Lindroth *et al.* 1973; Ball & Glucksman 1975) and nesting birds and other large animals may also locally contribute debris, animal remains and faeces to both littoral and terrestrial environments (Fridriksson 1987; Evans & Davy 2001). Furthermore, colonization of newly exposed substrates by aerially dispersed invertebrates, capable of surviving in and exploiting such environments, allows almost instantaneous establishment of simple but functional ecological communities. There is also now a broader recognition of the importance of allochthonous energy/nutrient cross-subsidies in the functioning of mature ecosystems (Polis *et al.* 1997) and, if we put these ideas together, there is a compelling case for rethinking our views on the early stages of community assembly on newly exposed inert substrates.

The role of grazing vertebrate animals in influencing the direction of the later stages of plant community assembly has long been recognized (Crawley 1983) but the more subtle importance of invertebrates in determining the balance between plant species and the speed of change has only more recently been recognized (Brown *et al.* 1988; Whelan 1989; Brown & Gange 1992; Bach 1994). Invertebrate 'successions' have often been studied in isolation from other successional processes taking place and their significance has been lightly touched on or not fully recognized (Majer 1989; Recher 1989; Miles & Walton 1993b). As a result invertebrates have generally been viewed as little more than adjuncts to plant community assembly, with the availability of soil and plants facilitating the gradual build up of an invertebrate community. We contend, however, that the functional significance of invertebrates, and their use of allochthonous inputs during the very earliest stages of primary community assembly, present serious gaps in our knowledge that warrant further examination. For

example, Mathews (1992), in a comprehensive review of primary 'succession' on glacier forelands, noted the absence of any relevant published data involving animals, a situation that has only lately been remedied (Kaufmann 2001; Kaufmann *et al.* 2002). A recent British Ecological Society Symposium (Miles & Walton 1993a) on terrestrial primary 'succession' was similarly conceptually constrained by a lack of detailed general information on animals or microbes, although the editors suggested that '... it is at the microscopic level that any consideration of primary succession must start.' Here we present evidence for the ecological significance of this initial heterotrophic stage of community assembly.

### Sources of organic materials

Deposition of windborne biological materials, in the form of living organisms or organic detritus onto the surface of well-vegetated terrain passes largely unnoticed. However, evidence from extensive studies on the aerial dispersal of plants and animals, especially insects and spiders, and the immigration into and colonization of remote islands or locations tells us that many biological organisms are highly mobile (Glick 1939; Pedgley 1982; Drake & Farrow 1988; Thornton 1996; Coulson 2000). For example, the remote subantarctic Macquarie and South Orkney Islands receive a rain of insects, pollen and organic debris originating in Australasia and South America (Salas 1983; Marshall 1996; Greenslade 1999). For living organisms, this is often a highly wasteful process, with most individuals failing to make a suitable landfall. These are the 'unlucky derelicts' of van Dyke (1919) and Edwards (1986b). We contend, however, that these organisms, when present at high densities, serve a highly useful ecological purpose by providing sources of energy, carbon and nutrients that together with wind-blown detritus, may power the earliest stages of primary community assembly on land. Windborne detritus originates as a decomposition product of plants and animals and through wind abrasion of living plants within established ecosystems (Rogge *et al.* 1993).

Evidence for significant deposition of these allochthonous materials is seen in the accumulation of living and dead organisms in traps on the surface of unvegetated terrain, on snow patches or on the surface of the sea, where they are more visually obvious and where they may act as a food source for other established organisms (see later).

### Invertebrate deposition

The accumulation of living and dead invertebrates on summer snowfields and glaciers enables one to estimate both the diversity and amount of inputs. Not unnaturally accumulation has been observed most frequently in those regions where snow cover persists well into the growing season, usually at high altitude or higher

**Table 1** Summary of arthropod deposition on snowfields, glaciers, the surface of the ocean and newly formed land surfaces. Abbreviations for invertebrate groups are Arenaea (A), Coleoptera (C), Collembola (Cl), Diptera (D), Dermaptera (Dm), Ephemeroptera (E), Hymenoptera (H), Homoptera (Ho), Heteroptera (He), Isoptera (I), Lepidoptera (L), Neuroptera (N), Orthoptera (O), Odonata (Od), Plecoptera (P), Psocoptera (Ps), Trichoptera (T), and Thysanoptera (Tp)

Site	Country	Groups recorded	Reference
<i>Snowfields &amp; glaciers</i>			
Mt Rainier, WA	USA	He + Ho, L, D, C, H	Van Dyke (1919)
Sierra Nevada, CA	USA	He + Ho, L, D, C, H	Van Dyke (1919)
Jungfrau	Switzerland	Cl, C, D and A	Heiniger (1989)
Pallas-Ounastunturi	Finland	H, D, C	Kaisala (1952)
Gulkana Glacier, AK	USA	Od, P, N, L, H, D, C	Edwards (1970)
Snowy Mountains, NSW	Australia	Ho, He, Tp, N, L, D, C, H	Edwards (1974)
White Mountain Peak, CA	USA	Ho, He, L, D, C, H	Spalding (1979)
Svalbard	Norway	Ho, D,	Elton (1925)
Cairngorm Mountains	Scotland	Cl, E, P, Ho, He, N, T, L, C, D, H and A	Ashmole <i>et al.</i> (1983)
Mt Teide, Tenerife	Spain	Ps, Tp, Ho, He, N, C, L, D, H and Ac	Ashmole & Ashmole (1988)
Mt Conness, Sierra Nevada, CA	USA	He, Ho, D, C, H and A	Papp (1978), Papp & Johnson (1979)
Eagle Summit, AK	USA	Tp, Ho, He, N, L, T, D, C, H	Edwards & Banko (1976)
Mt Rainier, WA	USA	A	Crawford & Edwards (1986)
Alps	Austria	Od, P, Ho, L, N, D, C, H	Liston & Leslie (1982)
Cairngorms	Scotland	C	Easton (1968)
Pyrenees	Spain	Tp, Ho, He, C, D, H	Antor (1994)
Knife Point Glacier, WY	USA	O	Lockwood <i>et al.</i> (1991)
<i>Ocean surface</i>			
English Channel		Cl, Ps, Tp, Ho, He, L, C, D, H	Cheng & Birch (1978)
Oregon Coast		Ps, Ho, He, N, L, C, D, H and A	Cheng & Birch (1978)
Gulf of California		Ps, Tp, Ho, He, N, C, L, D, H and A	Cheng & Birch (1978)
German Coast, North Sea		N, L, C, D, H	Heydemann (1967)
Atlantic off Tenerife		Cl, Is, Ps, Tp, Ho, He, C, D, H and A	Ashmole & Ashmole (1988)
<i>Land surface</i>			
W. Spitsbergen	Norway	D, L, H	Hodkinson <i>et al.</i> (2001) and unpublished
Anak Krakatau	Indonesia	Cl, O, Dm, Ps, He + Ho, L, C, D, H and A	Thornton <i>et al.</i> (1988)
Mt St Helens	USA	E, P, Ho, He, N, T, L, C, D, H and A	Edwards (1986a,b)

latitudes. Nevertheless, these tend to be nutrient-poor ecosystems in which invertebrate inputs may be most significant. Deposits (Table 1) have been observed that include the following hexapod orders: Collembola (Cl), Ephemeroptera (E), Plecoptera (P), Odonata (Od), Orthoptera (O), Psocoptera (Ps), Homoptera (Ho), Heteroptera (He), Isoptera (I), Thysanoptera (Tp), Neuroptera (N), Trichoptera (T), Lepidoptera (L), Diptera (D), Coleoptera (C) and Hymenoptera (H), together with spiders (Arenaea (A)). Observations from North America, Europe, Australia and the Himalayas, show that samples are highly variable, with different taxa predominant in different areas and at different times, i.e. inputs are largely probabilistic (Table 1). Some care, however, is needed in interpreting invertebrate snowfield communities, because the animals found may include both the vagrants and a permanent fauna comprising both predators and scavengers adapted for feeding on wind-blown invertebrates and/or detritus on the surface of the snow (Chapman 1954). The examples given attempt to exclude any indigenous fauna. Similar observations have been made on the deposition of invertebrates onto the surface of the sea and by sampling invertebrate inputs onto recently formed land surfaces (Table 1). Together these observations confirm the common

and widespread nature and diversity of ecologically significant fallout of invertebrates onto land and water surfaces and by inference onto successional terrain.

### Detritus deposition

By contrast with invertebrate deposition detritus deposition is frequently observed, often on snow, but is infrequently quantified (Fahnestock *et al.* 2000). Examination of detritus accumulated on snow or trapped on deposition (Table 2) demonstrates a wide range of aerially dispersed biological materials including leaf particles (L), pollen (P), spores (S), lichen (Lc), animal remains (A) (including both dead invertebrates and animal-derived products such as hair and feathers) and faeces (F). Frequently this biological material is mixed with fine inorganic particles (Welch *et al.* 1991; Shachak & Lovett 1998).

### Quantitative inputs of organic matter and nutrients

Invertebrates represent a particularly rich source of nutrients compared with detritus derived from plants. In particular, concentrations of the major macronutrients nitrogen (*c.* 10% by dry weight) and phosphorus

**Table 2** Summary of examples of deposition of allochthonous organic matter (excluding invertebrates) onto land surfaces. Materials deposited include Leaves (L), Seeds (S), Pollen (P), Lichen (Lc), Animal remains including feathers and hair (A), Faeces (F) and particulate organic detritus (D)

Substrate	Location	Country	Materials present	Reference
Snow	Devon Island	Canada	D	Teeri & Barrett (1975)
Snow	White Mountain Peak, CA	USA	L, S, P, Lc, A, F	Spalding (1979)
Snow	Jan Mayen	Norway	L, M, Lc	Warren Wilson (1958)
Snow	Cornwallis Island	Canada	L, M, Lc	Warren Wilson (1958)
Snow	Spitsbergen	Norway	L, Lc	Acock (1940)
Snow	Lapland	Finland	Not given	Kihlman (1890)
Snow	Ellesmere Island	Canada	D	Kawamura (1996)
Snow	District of Keewatin	Canada	D	Welch <i>et al.</i> (1991)
Glaciers	Alaska	USA	L, S, Diatoms	Kol (1942)
Tussock tundra	Alaska	USA	L	Fahnestock <i>et al.</i> (2000)
Unspecified	Signy Island	Antarctica	A	Marshall (1998)
Glacial moraine	Spitsbergen	Norway	L, Lc, S, A, F	Hodkinson <i>et al.</i> unpublished

(c. 1–3%) are several times higher in insects than in higher plants and similar positive disparity occurs in some micronutrients such as copper and zinc (Hodkinson & Hughes 1982).

There is little consistency or comparability in the methods used to measure invertebrate fallout by different workers, but the available data indicate the potential magnitude of the process. Mean standing crops of invertebrates on snowfields range from 5000 to  $15 \times 10^6$  individuals  $\text{ha}^{-1}$  at montane sites in Alaska, Australia, USA and northern Spain (Edwards 1970, 1974; Spalding 1979; Antor 1994). Mean daily input rates measured at other sites in the USA, Scotland and Indonesia ranged from 1 to  $20 \times 10^4$  individuals  $\text{ha}^{-1} \text{day}^{-1}$  (Papp 1978; Mann *et al.* 1980; Ashmole *et al.* 1983; Thornton *et al.* 1988). Nutrient addition, for yet other montane sites in the USA, has been calculated at between 0.05 and 0.82 kg N  $\text{ha}^{-1} \text{year}^{-1}$  and 0.002–0.06 kg P  $\text{ha}^{-1} \text{year}^{-1}$  (Edwards & Banko 1976; Edwards & Sugg 1993), although these rates are lower than the peak daily inputs of 2.65 kg N  $\text{ha}^{-1}$  and 0.20 kg P  $\text{ha}^{-1}$  calculated for a lowland glacial moraine in Spitsbergen (Hodkinson *et al.* 2001). As Hodkinson *et al.* (2001) pointed out, these latter amounts potentially exceed the rate of artificial fertilizer addition used in nutrient manipulation experiments at adjacent sites (Robinson & Wookey 1997).

Data for organic detritus inputs again lack clear comparability among sites. Quantities of organic material deposited on snow and other surfaces range from 3 to 350 kg  $\text{ha}^{-1}$ , with the proportion of organic material ranging between 1 and 100% (Warren Wilson 1958; Teeri & Barrett 1975; Spalding 1979). The only continuous record of aerial organic detritus input, estimated for sites on Mount St. Helens over several years, gives inputs ranging between 0.31 and 0.93 kg  $\text{ha}^{-1} \text{year}^{-1}$  (Edwards & Sugg 1993). Fahnestock *et al.* (2000) have recently recorded up to 1430 kg C  $\text{ha}^{-1}$  on snow patches in Alaskan tussock tundra, emphasizing the potential scale of detrital movement.

In absolute terms, rates of organic matter deposition are not particularly high but in the nutrient and energy

deficient habitats of early succession these inputs are clearly sufficient to sustain the newly established food webs described in the following section.

### Food web development and nutrient capture and concentration mechanisms

It is a significant feature of newly exposed substrates that the early animal colonisers (Table 3) are predators or scavenging detritivores/omnivores. Examples shown embrace a wide variety of natural substrates, including volcanic lava and ash, glacial moraine, scree slopes, sand dunes, polders and both marine and lacustrine littoral zones. Similar conclusions can be drawn for the industrially created substrates listed, such as coal spoil and clay-covered landfill sites. Furthermore, the successions cited span a broad range of climatic conditions from the high Arctic to the tropics. In addition to the important invertebrate groups previously noted, such as the beetles and spiders, the predators and scavengers also include Thysanura (Th) (= Archaeognatha), Grylloblattodea (Gr), Mantodea (M), Opiliones (Op), Acari (Ac), Chilopoda (Ch), Isopoda (I) and Nematoda (Nm) as well as protozoa such as Mastigophora (Ma) and testate amoebae (Am). Often the predators in particular are present at unusually high densities compared with more mature ecosystems (Hodkinson *et al.* 2001). Herbivores, despite their similar dispersal abilities, are conspicuously absent from the *established* community. The secondary consumers thus precede the primary consumers in the successional process, reflecting the nature of the available food sources. The predators, mainly spiders and beetles such as Carabidae and Cincindelidae, are able to maintain high numbers by feeding on wind-blown prey items and the detritivores such as Collembola and Dermaptera feed similarly on dead allochthonous organic materials, and presumably on the microorganisms associated with them. Together they serve as an efficient biological capture and concentration mechanism for nutrients, particularly nitrogen. These animals often actively select and occupy favourable sheltered

**Table 3** Examples of successional ecosystems in which invertebrate predators, parasitoids and or detritivores are established before colonization by higher plants and herbivores. Occasional examples are included where vegetation is exceedingly sparse yet an invertebrate community is broadly established. Abbreviations for invertebrate groups are: Araneae (A), Coleoptera (C), Collembola (Cl), Diptera (D), Dermaptera (Dm), Orthoptera (O), Hymenoptera (H) and Heteroptera (He) as before, together with Acari (Ac), Chilopoda (Ch), Grylloblattodea (Gr), Isopoda (I), Mantodea (M), Nematoda (Nm), Opiliones (Op), Thysanura (Th) (= Archaeognatha) and protozoa, namely testate amoebae (Am) and Mastigophora (Ma)

Substrate	Location	Country	Group	Reference
Glacial moraine	Spitsbergen	Norway	Cl, D, H and A	Hodkinson <i>et al.</i> (2001)
Glacial moraine	Rotmoosferner	Austria	C, A, Ac, Op	Kaufmann (2001, 2002)
Volcanic	Anak Krakatau	Indonesia	Cl, O, Dm, Ps, Ho + He, C, D, H and A	Thornton & New (1988)
Volcanic	Tenerife	Spain	Th, O, Dm, He, and A, Op, Ac, Ch	Ashmole & Ashmole (1987)
Volcanic	Lanzarote	Spain	Cl, Th, O, C, and A, Ac, I,	Ashmole & Ashmole (1987)
Volcanic	Capelinhos Azores	Portugal	Cl, Th, O, C, D, H and A, Ac and I	Ashmole <i>et al.</i> (1996)
Volcanic littoral	Surtsey	Iceland	Cl, D	Lindroth <i>et al.</i> (1973), Fridriksson (1975)
Sand	Lauwerszee Polder	Netherlands	A	Meijer (1971, 1977, 1980)
Mud banks	Florida Keys	USA	Cl, Dm, C	Simberloff & Wilson (1970)
Volcanic	Rakata, Krakatau	Indonesia	A	Cotteau (1885)
Volcanic	Mt Etna	Italy	A	Wurmli (1974)
Snow	Pallas-Ounastunturi	Finland	C, D and A	Kaisala (1952)
Snow	Himalayas	Nepal	A	Swan (1963)
Snow	Mt Conness, Sierra Nevada	USA	C	Papp (1978)
Snow	Mt Rainier	USA	Cl, C, G, and Op	Mann <i>et al.</i> (1980)
Volcanic	Kilauea Volcano, Hawaii	USA	Cl, O, Dm and I	Howarth (1979)
Volcanic	Mt St. Helens	USA	C, He, G, O	Sugg & Edwards (1998)
Volcanic	Anak Krakatau Hawaii	USA	O, M and A	Thomton <i>et al.</i> (1988), New & Thomton (1988)
Volcanic	La Palma	Spain	Cl, Th, O, D, H and A	Ashmole <i>et al.</i> (1992)
Volcanic	El Hierro	Spain	Cl, Th, O, D, H and A	Ashmole <i>et al.</i> (1992)
Sand dune	Slowinski National Park	Poland	Nm	Goralzyk (1998)
Volcanic	Mt St. Helens	USA	A	Crawford <i>et al.</i> (1995)
Scree	Dolomites	Italy	A and Op	Zingerle (1999)
Alkaline shale coal spoil	Alabama	USA	Cl and Ac	Cross & Wilman (1982)
Volcanic	Deception Island	South Shetland Is.	Ma	Smith (1985)
Sand dune	Tentsmuir & Whiteford	Scotland & Wales	A	Duffey (1968)
Mud bank	W. Australia	Australia	D, O, C, D, H and A and Ac	Woodroff & Majer (1981)
Coal shale	Northumberland	England	Cl	Hutson (1980)
Landfill covered by clay	Essex	England	Cl, C, A	Judd & Mason (1995)
Bare cays	Great Barrier Reef/Coral Sea	Australia	Cl, Dm, D, C, L and Ch, A, I, Ac	Heatewole (1971)
Clay bluff	Michigan	USA	C, H, A	Shelford (1913)
Sandy beach	Sar Uanle	Somalia	C	Chelazzi <i>et al.</i> (1983)
Sandy beach	Port Elizabeth	South Africa	C	Callan (1964)
Coal spoil	Berzdorf	Germany	Am, Ma	Wanner <i>et al.</i> (1998)
Coal spoil	Lower Lusatia	Germany	A	Mrzljak & Wiegleb (2000)

microhabitats and their defaecation and death, leading to decomposition, may begin the gradual process of soil formation and accumulation at selected microsites. Early spider colonists, especially Linyphiidae, may be especially important in that their horizontal webs, constructed on the substrate surface, capture detritus as well as prey and may also serve physically to stabilize the substrate surface (Hodkinson *et al.* 2001). The composition of the spider silk varies among species but consists predominantly of complex structural proteins (Vollrath 1999) and thus potentially distributes nitrogen over the substrate surface.

### Mechanisms of organic matter concentration

Airborne insects and detritus are not distributed uniformly over the landscape. Several mechanisms may act to concentrate and thereby localize the deposition of materials, leading to pockets of concentration. Often this involves simple physical processes, but in the case

of flying insects, the insects' behaviour may also be important. Mass synchronous take-off by dispersing insects can produce distinct plumes of aggregation, detectable by radar (Pedgley 1982). Concentration can also be further enhanced by active flight behaviour that produces convergence. For example, dispersing plumes of diamondback moth from W. Russia suddenly appeared on the high Arctic Svalbard in July 2000. They are thought to have been induced to land in a concentrated band along the west coast after sighting the land surface visible through broken cloud (Coulson *et al.* unpublished). Similarly dispersing insects in Florida concentrate over land along the coastline (Russell & Wilson 2001). There is a known tendency for many insect species to aggregate on mountain tops or in mating swarms, often over prominent topographical features (van Dyke 1919; Williams 1958; Hodkinson *et al.* 1996). Flying insect species also show characteristic patterns of concentrated deposition in the lee of windbreaks, resulting from both upwind and downwind

movements, depending on their size and flight ability (Lewis & Dibley 1970; Pedgley 1982).

By contrast with flying insects, deposition and concentration of wind-blown allochthonous detritus and passively dispersed animals depends almost entirely on physical processes. Nevertheless, some physical processes achieve similar ends. For example, in regions with heavy winter snowfall, detritus accumulates on the snow surface. Warren Wilson (1958) showed that during the subsequent summer shrinkage of snow patches by ablation this detritus tends to become concentrated towards the centre of the patch, leading to a concentrated area of deposition. Within the snow patch itself the differential melting of the surface produced by differential ablation produced by accumulated detritus produces 'dirt cones' that further concentrate detrital material into cone-shaped raised areas on the surface (Warren Wilson 1954). Dry conditions and wind can also further redistribute deposited material over the land surface, leading to accumulation in the sheltered lee of surface irregularities such as rocks (del Moral & Wood 1993a,b; Edwards & Sugg 1993; Fahnestock *et al.* 2000). These mechanisms thus act together to ensure the aggregation of allochthonous materials in particular microsites.

Why is allochthonous material so important? Colonization of apparently barren terrain by higher plants necessitates the plant establishing a foothold in an otherwise hostile environment. The availability of suitable microsites has been shown to be an important prerequisite for the plant establishment (Griggs 1933; Blundon *et al.* 1993; del Moral & Bliss 1993; Castellanos *et al.* 1994) and recent attempts have been made to characterize these sites (Jumpponen *et al.* 1999). The sites of nucleation, such as surface depressions and cracks, appear similar to those favoured by invertebrates and are likely to be the points at which organic materials, decomposer organisms and nutrients are most likely to concentrate both through invertebrate activity and other physical processes (Titus & del Moral 1998). The concept of facilitation is often employed when considering plant succession (Chapin *et al.* 1994; McCook 1994; Callaway 1995; Lichter 2000). It is used to describe the presence of one plant species favouring the establishment of another plant species. We contend that the concept needs to be broadened to include animal facilitation in which the presence of simple animal communities at the very earliest stages of succession, supported by allochthonous inputs of organic matter, create the conditions favourable for plant establishment. Their presence may help to create microsites with improved substrate moisture characteristics and enhanced nutrient availability, which also may serve as sites for later mycorrhizal inoculation.

### Temporal and spatial considerations

Clearly the rate and timing of both living and dead organic matter inputs into a particular site will depend

on many factors. These will include, in particular, the availability of suitable wind-dispersible materials, their proximity and dispersability, and the direction and speed of both prevailing and local winds (Taylor 1986; Burt & Pedgley 1997). Upward convection and turbulent motion of the atmosphere is important for long-distance dispersal (Drake & Farrow 1988), whereas local microclimate will determine the flight take-off activity of insects (Peng *et al.* 1992). Recent advances in radar technology now allow the continuous quantitative monitoring of small aerially dispersing insects over selected landscapes (e.g. Beerwinkle *et al.* 1994; Smith *et al.* 2000). This opens up the possibility that the quantities of dispersing insects can be modelled and, given certain basic input parameters, predicted (Yang *et al.* 1998).

### Time scales for community assembly

The time interval before the heterotrophic early stage of community assembly is overtaken by autotrophic succession will clearly vary. It will depend on time, temperature, moisture and nutrient/energy input rate. In warm climates with adequate moisture it may take but a matter of weeks. In cold climates, or those lacking adequate moisture, the process will be slower and the heterotrophic phase may persist for several years. For example, on nutrient-poor moraines on Spitsbergen we estimated this period to be about 16 years. At extreme altitudes or under extremely arid conditions colonization by higher plants may be restricted by the climatic extremes and the heterotrophic stage might persist indefinitely. Climatic amelioration, however, might ultimately allow community assembly to proceed in the usual manner.

### Conclusions

The ecological literature contains many disparate and often neglected observations relevant to our understanding of the initial stages of community assembly on land, but little attempt has been made to draw them together into a coherent framework. There is strong evidence to suggest that heterotrophic communities, supported by allochthonous inputs of invertebrates and other organic particles, represent the earliest stages of primary community assembly in a wide range of terrestrial ecosystems. These communities have received little acknowledgement in the development of theoretical ideas relating to community assembly, despite their possible role as initial facilitators of the autotrophic 'successional' process. There is a strong need to integrate these concepts more fully into mainstream ecology. The functional significance of these processes of initial community assembly, especially the microbiological aspects, are under-researched and will remain so until ecologists become willing to extend their sphere of activity from the interesting to the functionally important (Wilkinson 1998).

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