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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Are high Arctic terrestrial food chains really that simple? – The Bear Island food web revisited

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Summerhayes and Elton's (1923) "nitrogen cycle" diagram for Bear Island (Bjørnøya), Svalbard, is widely used to illustrate the organisation of high Arctic food webs. We present a revision of the terrestrial section of this food web based on 12 years work on Spitsbergen, Svalbard. The level of complexity is much greater than Summerhayes and Elton suggested and the implications for ecological theory are discussed. In particular the low level of primary productivity does not appear to restrict the length of ectotherm food chains. This may in part be due to the open nature of the ecosystem, which receives energy/nutrient subsidies in the form of allochthonous wind-blown insects and detritus, particularly from surrounding aquatic environments. Connectivity is also significantly higher. Our data support the increasingly accepted view that many food webs presented in the literature are gross oversimplifications and that analysis of their structure can produce misleading conclusions.

The ecological literature contains many examples of unresolved, partially resolved or incomplete food webs in which major assemblages of species often are aggregated into single units and their constituent species thereby relegated into functional obscurity. Such webs are highly misleading with respect to biodiversity, food chain length, connectivity and regulation of energy flow (Martinez 1993, yet analyses of their structure has often formed the basis of food web theory (Pimm and Lawton 1980, Pimm 1982, Cohen 1990). Several recent analyses and comparisons of food webs within a range of ecosystems, from deserts and low Arctic tundra to estuaries and lakes, highlight the underlying problems associated with the study of unresolved webs (Hall and Raffaelli 1991, Martinez 1991, Polis 1991, Oksanen et al. 1996, 1997). In particular, mean chain length, apparent compartmentalisation and the links per species ratio decrease as species are aggregated. In parallel, the proportions of top and basal species tend to increase (Martinez 1993). Quantitative parameters thus vary significantly with the level of resolution employed, suggesting that reliable measurements can only be made on fully resolved webs.

A prime example of an unresolved food web, yet one considered a foundation study in trophic ecology, is Summerhayes and Elton's (1923) "nitrogen cycle" diagram for Bear Island (Bjørnøya), Svalbard, which was later reproduced as a "food cycle" in Elton's (1927) seminal book Animal Ecology. This basic diagram has subsequently been copied or modified in many text books up to the modern day and the underlying characteristics of the relatively simple Arctic 'food web' have been widely accepted into general ecological theory (Pimm and Lawton 1980, Pimm 1982, Colinvaux 1993, Begon et al. 1996, Morin 1999, Molles 2000, Rickleffs and Miller 2000). Despite the criticisms highlighted above, similar simplifications of Arctic terrestrial food webs, dominated by vertebrates, continue to appear (Krebs et al. 2003).

We here suggest that Elton's Arctic 'food web' diagram is a generalization, designed primarily to illustrate major pathways of nutrient/energy flux and the interdependence between the terrestrial and aquatic ecosystems, rather than to detail the intricate food web relationships. Perusal of the results of the Oxford University Expeditions, to which Elton was a major contributor, confirms that Elton was aware of a much more complex Arctic food web structure than that illustrated (Morice 1922, Jackson 1922, 1925, Stephenson 1922, Collin 1923, Waterston 1923, Elton 1925, 1929, Summerhayes and Elton 1928). These early papers indicate the presence of many invertebrate groups excluded from the food web diagram and illustrate the species richness and trophic diversity hidden within broad headings such as 'Hymenoptera' or 'Diptera'. Many subsequent faunal studies on Svalbard (summarised by Coulson and Refseth 2004) strongly reinforce these conclusions yet the myth of Arctic simplicity persists. There is often a failure to fully appreciate that Summerhayes and Elton's diagram operates at different taxonomic levels for vertebrates (species) and invertebrates (mainly Order or Class), such

that among animals vertebrate links appear predominant. This makes any conclusions regarding the length of food chains and connectivity of food webs highly unreliable (Stiling 2002).

Table 1 illustrates the 'true' species richness of selected Svalbard terrestrial invertebrates, showing that the five invertebrate 'trophic boxes' used by Summerhayes and Elton, namely Collembola, Diptera, mites, Hymenoptera and spiders, comprise upward of 300 species within the Svalbard archipelago. Similarly, within the Protozoa box there are 188 species of testate amoebae, displaying a wide trophic diversification: the terrestrial 'worms' (Enchytraeidae) again number over 30 species. Other significant groups of insects omitted from the diagram include herbivorous and predatory beetles (Coleoptera), plant bugs (Hemiptera), moths (Lepidoptera), parasitoid wasps (Hymenoptera), lice (Phthiraptera = Anoplura + Mallophaga) and fleas (Siphonaptera). Vascular plants also number 165 species (Elven and Elvebakk 1996). These data, however, like Summerhayes and Elton's original diagram, apply to broad geographical areas and all species are unlikely to occur together at the same place and time. To give a better appreciation of how these species are structured within a functioning community it is necessary to establish the species interrelationhips within a small defined area.

For the past 12 years we have worked on invertebrate communities on W. Spitsbergen (500 km N of Bear Island), Svalbard and are now able to contribute a more detailed and realistic terrestrial food web based on a variety of published and unpublished data. Figure 1 and 2 presents the detailed food web for an area of around 2 km^2 adjacent to Ny-Ålesund, W. Spitsbergen Svalbard, incorporating the proglacial areas of Midtre Lovénbreen (a glacier) and an area of mature vegetation that has been undisturbed by glaciation for around 2000 years (Coulson et al. 2003a, Hodkinson et al. 2003a). It is based on information gathered during intensive sampling programmes extending over several years

(Hodkinson et al. 1996, 1998, 2003a, b, 2004, Coulson et al. 2002, 2003a, b, unpubl.). The emphasis is on soil-dwelling and free-living terrestrial invertebrates, particularly arthropods (Fig. 1). The unidentified terrestrial chironomids are grouped in a single box that probably contains between 1–3 species, including Smittia spp. (Sendstad et al. 1976). Soil nematodes and ciliates still remain largely unknown. The simpler vertebrate food web (Fig. 2) is shown separately for comparison. We are also acutely aware that by moving just a short distance out of the defined area, into marginally warmer or wetter/drier habitats, we can immediately begin to expand significantly the species pool and thus the complexity of the web.

The food web retains the essential structure of Elton's original, with the recognition of the high importance of energy/nutrient transfer into the terrestrial compartment in the form of insects, predominantly several species of Diptera, often of freshwater aquatic origin. It also recognises that at least in some years this may also involve mass long-range wind immigration of insects, such as the moth Plutella xylostella, from the European mainland (Coulson et al. 2002). Such energy/nutrient subsidies are increasingly recognised as an essential element supporting the trophic structure of the community (Polis et al. 1997, Hodkinson et al. 2002). The web is organised with compartments representing the primary producers, and the organic matter resulting from their death and decomposition, lying at the base. Inputs of allochthonous insects are indicated in the top left corner by the bold arrow. The flow of energy and nutrients along food web pathways is generally from bottom to top, with species of equivalent higher trophic position occupying the successive horizontal layers.

The main features of this food web that distinguish it from that of Summerhayes and Elton are the greatly increased number of species, the higher levels of connectivity among species and the significantly longer food chains. Furthermore, there is some indication of compartmentalisation within this terrestrial web. In particular the invertebrate herbivore food chains are largely segregated on single plant species and there is a specialist decomposer feeding on reindeer dung. Further work may reveal greater specificity of particular species lying within the cryptostigmatic mite and Collembola boxes. There is, for example, some evidence that the composition of soil microarthropod communities is influenced by plant species distribution within the vegetation mosaic (Coulson et al. 2003c). Another noteworthy feature is the significant number of hymenopterous parasitoid species, including some groups that are known as hyperparasitoids. This leads to the conclusion that despite the exceedingly low levels of primary production the system appears capable of supporting long (up to 6–7 link) food chains, providing little support for the idea that average chain length is limited

Table 1. Species richness of selected terrestrial invertebrate taxa for the Svalbard archipelago (from Coulson and Refseth 2004, with additions). Among Diptera, particularly chironomidae) many species are aquatic as larvae but free flying as adults.

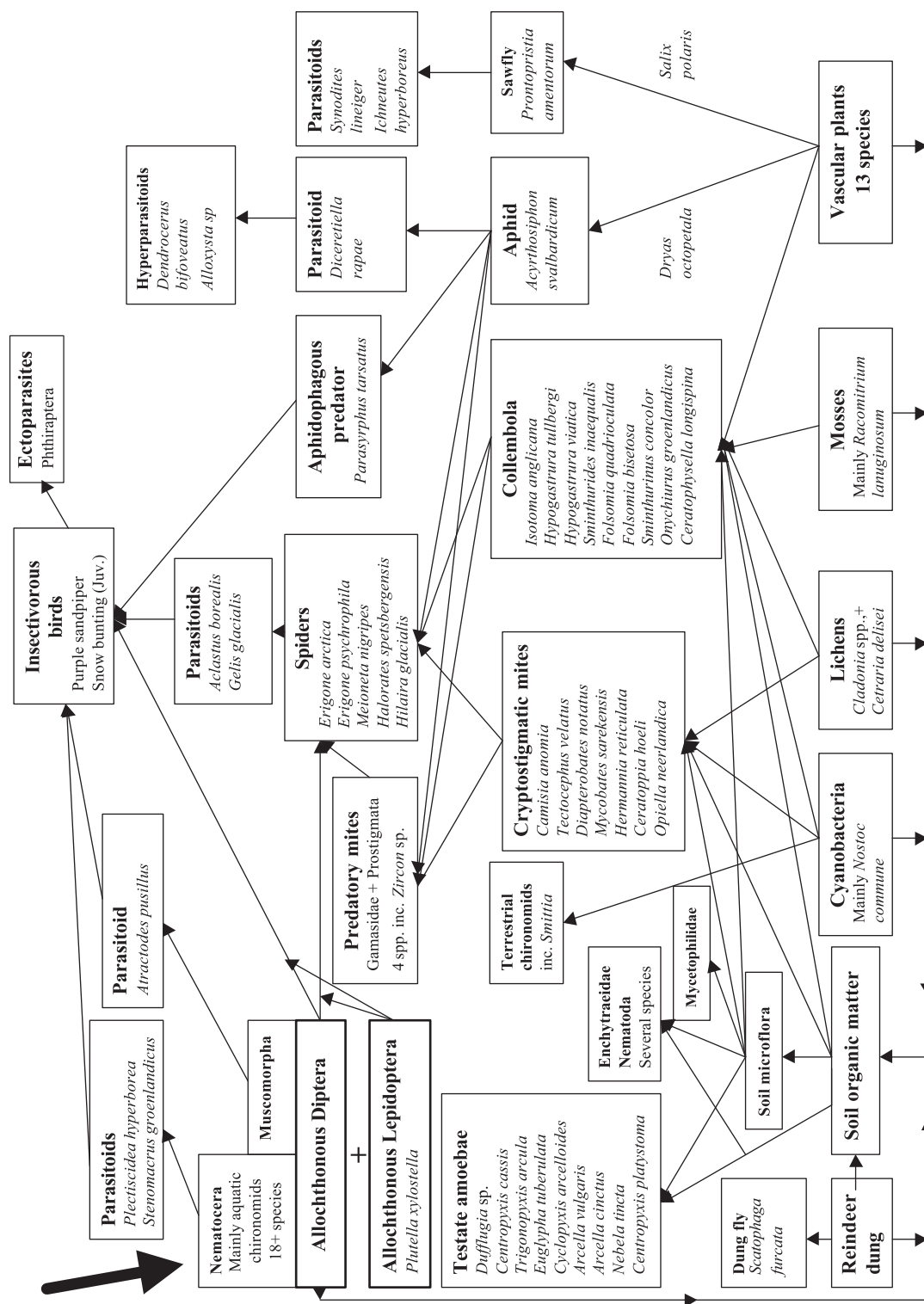| Invertebrate group	Svalbard species
Hemiptera	4
Coleoptera	19
Diptera	128 (as adults)
Hymenoptera	26
Lepidoptera	11
Arachnida: Acari	
Acariformes	98
Parasitiformes	18
Arachnida: Araneae	18
Collembola	59
Phthiraptera	39
Siphonaptera	2
Testate Amoebae	188
Oligochaeta, Enchytraeidae	34

Fig. 1. Revised terrestrial invertebrate food web diagram for a site adjacent to Ny-Ålesund, Spitsbergen, Svalbard. Sources of information are summarised in the text. The large black arrow indicates inputs into the system from adjacent or distant areas. Some less important arrows from dung flies, terrestrial chironomids and Mycetophilidae etc. to insectivorous birds are omitted to prevent over-complication.
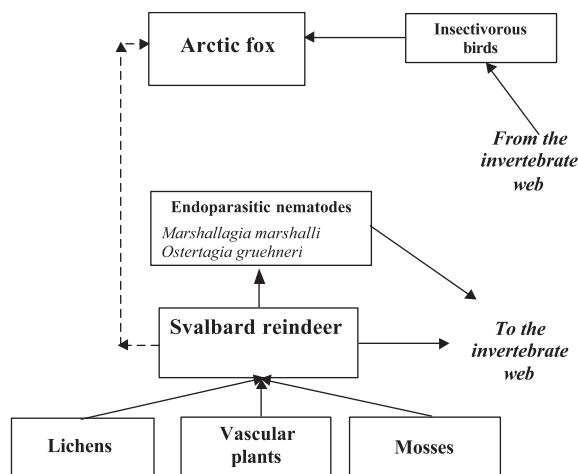
Fig. 2. Vertebrate food web linking to Fig. 1. The link between reindeer and Arctic fox is intended to suggest a donor relationship based on scavenging of carcasses and placentas.

by primary productivity. The increased length of the food chain, coupled with the higher connectivity, may also have implications for food web stability, although this remains a contentious area (Pimm 1982, Sterner et al. 1997).

Another important point that is often overlooked is that apparently equivalent compartments of the food web may turn over at greatly different rates. This is apparent in our diagram. The aphid *Acyrthosiphon svalbardicum* has up to three generations per year, the sawfly *Prontopristia amentorum* has a 1-year life cycle, a few Collembola have 2-year cycles and some cryptostigmatic mites take several years to reach maturity (Strathdee et al. 1993, Birkemoe and Leinaas 1999, Søvik and Leinaas 2003 and unpubl.). Irrespective of population sizes, energy and nutrients will thus flow at dissimilar rates through different parts of the web.

Some conclusions can also be drawn about the relative length, complexity and regulation of vertebrate (endotherm) and invertebrate (ectotherm) herbivore food chains. The vertebrate grazing chain (Fig. 2), based on Svalbard reindeer, is short, straight and not regulated by vertebrate predators, as might be predicted from the low level of productivity (Fraser and Grime 1997, Oksanen and Oksanen 2000). Predation by the top predator, the polar bear, is negligible in west Spitsbergen and it is the invertebrate ecto- and endoparasites that predominantly exploit reindeer production. There is now growing evidence that Svalbard reindeer populations may, however, be regulated by their nematode endoparasite burden, acting through effects on reproductive rates (Stien et al. 2002). Arctic fox may act as both a top predator, taking insectivorous birds such as purple sandpiper, but also as a recipient, through scavenging, of energy from this vertebrate herbivore donor food chain. By contrast, the invertebrate herbivore food

chains (Fig. 1) are significantly longer, more compartmentalised, more complex and with the strong possibility of top regulation by invertebrate predators and parasitoids. The web, however, is dominated numerically by oligopahagous consumer species feeding on dead organic matter and its associated microflora, again with potential regulation from predators such as spiders and predatory mites.

To conclude, the Svalbard high Arctic terrestrial food web is far more complex than has previously been appreciated but further sections remain to be resolved. Analyses and interpretations based on the simple structure shown by Summerhayes and Elton are likely to be misleading. The contribution of Arctic terrestrial trophic systems to our understanding of food web theory requires revision.

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