BIOLOGICAL REVIEWS
Cambridge Philosophical Society

Biol. Rev. (2013), **88**, pp. 327–348.
doi: 10.1111/brv.12002

Invertebrates, ecosystem services and climate change

Chelse M. Prather[1,2,3,*], Shannon L. Pelini[4,5,†], Angela Laws[6,7,†], Emily Rivest[8,9], Megan Woltz[10,11], Christopher P. Bloch[3,12], Israel Del Toro[4,13], Chuan-Kai Ho[14,15], John Kominoski[16,17], T. A. Scott Newbold[18], Sheena Parsons[6,7] and A. Joern[6,7]

[1] *Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46637, USA*
[2] *Department of Biology and Biochemistry, University of Houston, Houston, TX 77004, USA*
[3] *Luquillo LTER, Río Grande, Puerto Rico, PR 00945, USA*
[4] *Harvard Forest (HF LTER), Harvard University, Petersham, MA 01366, USA*
[5] *Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA*
[6] *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
[7] *Konza Prairie LTER, Manhattan, KS 66506, USA*
[8] *Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106, USA*
[9] *Moorea Coral Reef LTER, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA*
[10] *Department of Entomology, Michigan State University, East Lansing, MI 48912, USA*
[11] *W. K. Kellogg Biological Station LTER, Hickory Corners, MI 49060, USA*
[12] *Department of Biological Sciences, Bridgewater State University, Bridgewater, MA 02325, USA*
[13] *Department of Biology, University of Massachusetts Amherst, Amherst, MA 01003, USA*
[14] *Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 106, Taiwan*
[15] *Georgia Coastal Ecosystems LTER, University of Georgia, Athens, GA 30602, USA*
[16] *Department of Biological Sciences, Florida International University, FL 33199, USA*
[17] *Odum School of Ecology & Coweeta LTER, University of Georgia, Athens, GA 30602, USA*
[18] *Department of Life Sciences, Sheridan College, Sheridan, WY 82801, USA*

ABSTRACT

The sustainability of ecosystem services depends on a firm understanding of both how organisms provide these services to humans and how these organisms will be altered with a changing climate. Unquestionably a dominant feature of most ecosystems, invertebrates affect many ecosystem services and are also highly responsive to climate change. However, there is still a basic lack of understanding of the direct and indirect paths by which invertebrates influence ecosystem services, as well as how climate change will affect those ecosystem services by altering invertebrate populations. This indicates a lack of communication and collaboration among scientists researching ecosystem services and climate change effects on invertebrates, and land managers and researchers from other disciplines, which becomes obvious when systematically reviewing the literature relevant to invertebrates, ecosystem services, and climate change. To address this issue, we review how invertebrates respond to climate change. We then review how invertebrates both positively and negatively influence ecosystem services. Lastly, we provide some critical future directions for research needs, and suggest ways in which managers, scientists and other researchers may collaborate to tackle the complex issue of sustaining invertebrate-mediated services under a changing climate.

Key words: climate change, insects, invertebrates, ecosystem services, sustainability, biodiversity, ecosystem engineers, bioindicator species.

---

[*] Address for correspondence (Tel: (859) 466–4044; Fax: (713) 743–2636; E-mail: chelse.prather@gmail.com).

[†] Authors contributed equally.

CONTENTS

I. INTRODUCTION

Climate change is currently altering ecosystem services (e.g. primary production – Melillo *et al.*, 1993; water flux and quality – Vorosmarty & Sahagian, 2000), which are the supply of benefits from ecosystems to society that support human life and well-being (Chan *et al.*, 2006). As a result, politicians, land managers, researchers and the general public all have vested interests in better understanding how to conserve ecosystem services under a changing climate. Global efforts to examine the magnitude and rate of climate change (e.g., Intergovernmental Panel on Climate Change, IPCC) and the consequences for ecosystem services (Millennium Ecosystem Assessment, MA; Carpenter *et al.*, 2009; Naeem *et al.*, 2009; Mooney, 2010) have not yet linked with efforts to understand declines in biodiversity (International Union for the Conservation of Nature, IUCN and its newly formed program, the Intergovernmental Platform on Biodiversity and Ecosystem Services), which encompasses the organisms that affect ecosystem services (cf., Parmesan, 2006).

There is still a general lack of understanding regarding how the loss of particular species or groups of species will affect ecosystem services (Balmford *et al.*, 2011). Although invertebrates influence these valuable services, the general public either often disregards the roles of many invertebrates (Snaddon, Turner & Foster, 2008) or views them negatively, 'with aversion, anxiety, fear, avoidance, and ignorance', largely because some invertebrates cause diseases and crop damage (Kellert, 1993). Invertebrates are likely to be important for ecosystem service conservation because they fill many niches as the most globally abundant and diverse animal group, comprising over 80% of the 1.6 million described eukaryotic species (Brusca & Brusca, 2002), and estimates of invertebrate biomass, especially in complicated systems such as rainforests, continue to climb (Elwood & Foster, 2004). Invertebrates are also highly responsive to climate change, and their responses to recent climate change have been well documented in terrestrial, marine and freshwater systems (e.g., Southward, Hawkins & Burrows, 1995; Hogg & Williams, 1996; Sagarin *et al.*, 1999; Bale *et al.*, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Zvereva & Kozlov, 2006; Durance & Ormerod, 2007). These responses include changes in geographic distributions, population size, phenology, behavior, and genetic composition (Parmesan, 2006). In addition, because invertebrates occupy a variety of trophic levels, they interact with many trophic groups, from primary producers to top predators, and therefore likely will have large indirect impacts on ecosystem services under global change (Traill *et al.*, 2010).

Although many ecologists may agree that invertebrates influence ecosystem services, there is a critical need to identify which services invertebrates impact and quantify the magnitude of their influence. To date, reviews of invertebrate influences on ecosystem services focus on a specific set of ecological systems (ground water- Boulton *et al.*, 2008; freshwater- Covich, Palmer & Crowl, 1999; agricultural systems- Isaacs *et al.*, 2009; soil- Lavelle *et al.*, 2006; see Schowalter, 2011 for a more general review). Furthermore, management of ecosystem services and large-scale syntheses of ecosystem services do not always explicitly include consideration of invertebrates and particularly their beneficial effects. For example, the MA primarily considers invertebrate disservices (e.g., disease transmission, crop damage; WRI, 2003). Similarly, the 2007 IPCC Working Group II devoted to ecosystem services (chapter 4) only mentions invertebrate effects on terrestrial ecosystem services in relation to tree pest species (Fischlin *et al.*, 2007). Yet, understanding how ecosystem services will be affected under future climate change scenarios first requires an understanding of all the key players providing those services.

Here, we first conduct a series of systematic literature searches to identify knowledge gaps in research regarding invertebrates, their effects on ecosystem services, and how their effects might be influenced by climate change. We then briefly describe how invertebrates respond to climate change, in invertebrate particular traits that are associated with high vulnerabilities to climate change. We then review the ecosystem services that invertebrates affect positively and negatively through both direct and indirect mechanisms. In doing so, we highlight representative examples from a variety of taxonomic groups and ecosystems. We describe the several cases in which climate change alterations of invertebrate-mediated services have been examined. Lastly, we highlight critical areas of research needed to understand how changes to invertebrate populations predicted with climate change will affect ecosystem services, and how conservation may be guided by keeping these invertebrate-mediated effects in mind.

II. KNOWLEDGE GAPS IN RESEARCH REGARDING INVERTEBRATES AND HOW THEIR EFFECTS ON ECOSYSTEM SERVICES MAY BE AFFECTED BY CLIMATE CHANGE

We conducted a series of searches on Web of Science to determine knowledge gaps in the literature about invertebrates, climate change and ecosystem services. We determined: (*i*) the relative number of papers out of the hits that were returned that measured invertebrate community structure (biomass, density, etc.), some type of climate measurement (temperature, precipitation, water pH, etc.), and an ecosystem service (see Section IV); and (*ii*) whether relevant hits were skewed across invertebrate groups, locations, journals, and ecosystem services.

We first conducted 34 Web of Science searches to determine the relative number of papers that measured an ecosystem service compared to the number that measured the effect of an invertebrate on each ecosystem service (Table 1). We used each ecosystem service that we discuss in Section IV (Table 5), with either climat* change* or climat* change* and invertebrat* (see Table 1 for search terms). We recorded the number of hits for each ecosystem service to determine this information. Next, we conducted 36 more Web of Science searches, all with 3 search terms (see search terms in Table 2) to determine the relative number of invertebrate-related papers that measure climate change and invertebrate influences on ecosystem services, and how these papers were spread across invertebrate groups, year of publication and continents. We used either ecosystem service* or ecosystem process, climate change* or global warm*, and either invertebrat* or one of each invertebrate phylum. For comparison, we also conducted these searches, and the five taxonomic kingdoms for some measure of how this type of research might be spread across higher taxonomic levels. For each of these hits, we determined whether the paper measured one of the three categories we were interested in (invertebrates, climate change, or an ecosystem service). If the paper did include relevant data, we recorded the year of publication, journal (see online Table S1 for results), the service measured, the type of climate change investigated, the invertebrate group, what biome and continent the research was conducted in, and which of our three categories the paper contained data about.

We recognize that there are some limitations with these types of searches, especially as our searches may miss many relevant papers. These searches are certainly biased by studies referring to groups of invertebrates (i.e. those that would have ‘invertebrate’ in the title or keywords) rather than individual species or groups that may not produce hits when we search for ‘invertebrat*’ (e.g., pollinators). Our methods may also miss papers that refer to an ecosystem service by the name of the service (e.g. seed dispersal), but not by ‘ecosystem service’. However, as our main goal is to demonstrate gaps in knowledge, we feel that the data we collected are sufficient to do this.

Table 1. Number of hits from Web of Science searches using different search terms: each service in the first column was used as a search term in combination with climat* change*, or climat* change* and invertebrat*

Service search term	climat* change*	climat* change* + invertebrat*
ecosystem service*	1155	22
ecosystem process*	4335	104
primary product*	3581	38
seed dispers*	449	6
pollinat*	385	6
decompos*	2580	51
nutrient cycl*	1485	33
Hydrologic flux	282	0
habitat modif*	448	30
bioturbat*	210	13
bioero*	31	1
natural product*	2423	25
Water quality	3070	61
Food web stability	56	5
disease regulat*	137	5
pest control*	218	7
recreation*	416	6

Although these searches have some limitations, the search did point out many knowledge gaps. First, we find that while many papers examine ecosystem services, very few of those papers also focus on invertebrates (Table 1). In fact, the number of hits when invertebrates are included ranged from 1 to 6% of the total number of hits for the ecosystem service alone. The second round of searches revealed other knowledge gaps. The plant kingdom produces many more hits for all searches than the animal kingdom (of which the invertebrates make up the largest proportion; Table 2). The 203 non-duplicated hits (see online Appendix S1) from these 36 searches suggest that this type of research seems to be disproportionately spread across invertebrate phyla (e.g., many more hits in nematodes and arthropods than other phyla, Table 2).

Fifty-one papers (25%) contained relevant data (measured one out of our three categories). These relevant papers have generally increased in time (Figure 1). The relevant papers are not evenly spread across the globe, with the majority of research conducted in Europe or North America, and a large proportion, mainly reviews, were not restricted to particular geographic regions (Figure 2). Slightly more studies were conducted in terrestrial systems (58%) than aquatic systems (42%). The aquatic studies, however, were mostly from marine systems; only five were conducted in freshwater systems, and these were all stream ecosystems. The 29 terrestrial studies represented a wider, but still limited, variety of ecosystems: 9 forest-related papers, 8 grass-dominated systems, 2 deserts, 2 agricultural systems, and the rest either multiple ecosystems or global reviews. Very few relevant papers actually measure something about invertebrates, climate change, and ecosystem services simultaneously (only 15 papers, or 7.3% of our original 203 hits). Interestingly, these papers were not spread evenly across ecosystem services: 11 measured decomposition rates, and 5 provided some measure of food web stability.

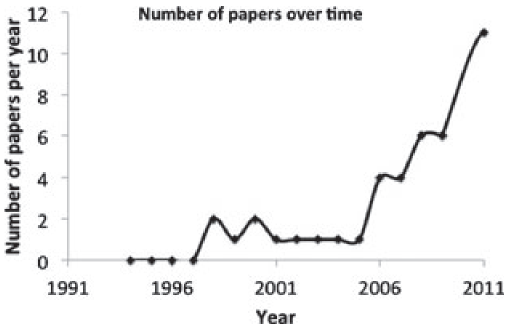

Fig. 1. Number of papers relevant to invertebrates, ecosystem services, and climate change over time from Web of Science searches.

Fig. 2. Distribution of papers relevant to invertebrates, ecosystem services, and climate change over continents from Web of Science searches.

All of this information demonstrates some fundamental knowledge gaps in research regarding how invertebrates affect ecosystem services, and how these effects may be altered by climate change. Out of all the hits in these searches, very few measured invertebrate communities, climate, and an ecosystem process simultaneously. In general, the relevant papers mostly looked at arthropods in terrestrial systems or corals in marine systems. This literature appears to have wide knowledge gaps in many areas including: highly managed terrestrial ecosystems, non-arthropod terrestrial invertebrates, non-coral marine invertebrates, and most freshwater systems (especially lakes and wetlands). We found that very little research about how invertebrate-influenced ecosystem services will be affected by climate change regions outside of Europe and North America. Not only is the literature usually focused on certain locations, ecosystems and invertebrate groups, but most of the literature thus far has focused on either supporting ecosystem services (see Section IV; primary production, nutrient cycling or decomposition) or food web stability. Below we provide a brief review of how invertebrates respond to climate change (as this topic has been thoroughly studied and extensively reviewed previously), followed by a more in-depth

Table 2. Number of hits from Web of Science searches using different search terms: either ecosystem service* or ecosystem process was used with a search term for climate change (climat* change* or global warm*) and each invertebrate phyla

Search terms			Number of hits	Kingdom	Number of hits
ecosystem service*	climat* change*	invertebrat*	20	animal*	132
		porifer*	0	plant*	260
		cnidar*	2	bacteria*	11
		platyhelminth*	0	fung*	13
		nematod*	4	*bacteria*	13
		echinoderm*	1	protist*	1
		mollus*	5		
		annelid*	1		
		arthropod*	6		
	global warm*	invertebrat*	8	animal*	30
		porifer*	0	plant*	45
		cnidar*	1	bacteria*	6
		platyhelminth*	0	fung*	3
		nematod*	2	*bacteria*	6
		echinoderm*	1	protist*	0
		mollus*	1		
		annelid*	1		
		arthropod*	2		
ecosystem process*	climat* change*	invertebrat*	109	animal*	448
		porifer*	2	plant*	1375
		cnidar*	8	bacteria*	140
		platyhelminth*	0	fung*	114
		nematod*	29	*bacteria*	171
		echinoderm*	4	protist*	9
		mollus*	8		
		annelid*	1		
		arthropod*	26		
	global warm*	invertebrat*	19	animal*	76
		porifer*	0	plant*	232
		cnidar*	1	bacteria*	41
		platyhelminth*	0	fung*	24
		nematod*	5	*bacteria*	45
		echinoderm*	1	protist*	1
		mollus*	0		
		annelid*	1		
		arthropod*	3	—	—

The same combinations of search terms were used with each kingdom of organisms for comparison.

overview of how invertebrates affect ecosystem services, before identifying where and how crucial research can inform conservation decisions to mitigate diminished invertebrate-affected ecosystem services.

III. INVERTEBRATES ARE HIGHLY RESPONSIVE TO CLIMATE CHANGE

Invertebrates are affected directly by abiotic conditions that are altered by climate change and indirectly by altered biotic relationships under climate change. The abiotic conditions that impact invertebrates under climate change differ depending on substrate. The effects of temperature change on aquatic invertebrates are accompanied by their responses to altered water chemistry and flow. For example, acidification in stream systems has significantly reduced the abundance of caddisflies, which alone could account for 37% of leaf litter breakdown, the basic ecosystem process in woodland streams (Simon, Simon & Benfield, 2009). Acidification can also affect marine organisms, for example, by reducing the survivorship of brittle stars, which function as a keystone species in regional food webs (Dupont *et al*., 2008). Acidification will also likely damage the diversity and structure of coral reefs (Walther *et al*., 2002). Furthermore, other consequences of climate change, like sea level rise, have important effects on invertebrates: sea level rise will likely outpace the growth of reef islands, creating unsuitable habitats for current, resident organisms (Wilkinson, 1996). Similarly, below-ground terrestrial invertebrates, which contribute to decomposition and above-ground productivity,

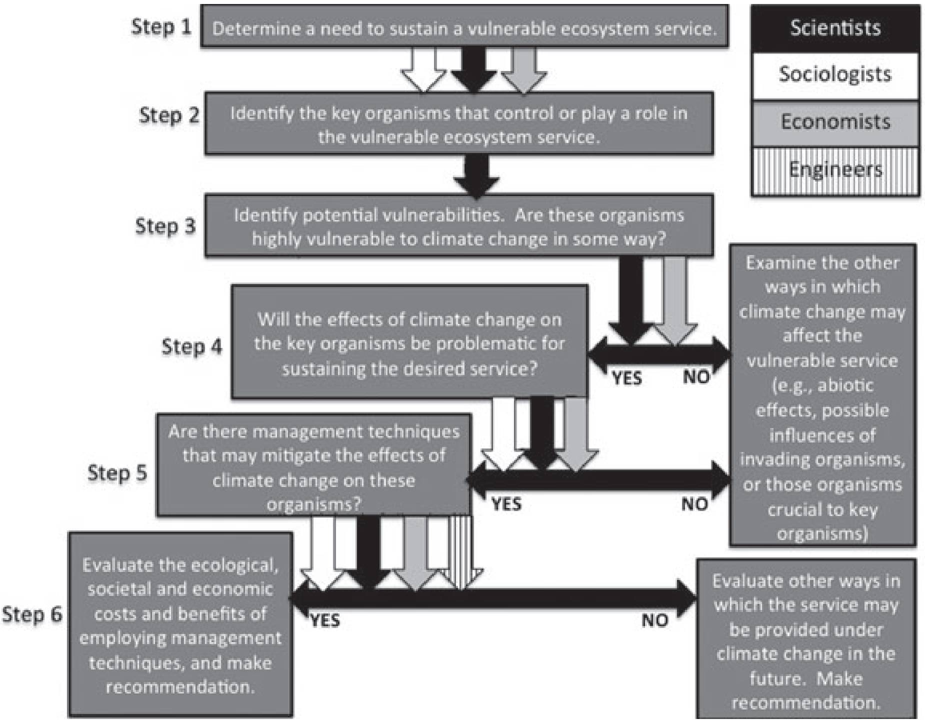

Fig. 3. A decision tree to identify when key organisms can be managed to sustain a vulnerable ecosystem service. Arrows are used to identify when researchers from different disciplines may have input in answering questions.

will respond to altered air and soil temperature, soil moisture, and thaw depth and timing (Wall, 2007).

Climate change may fundamentally alter many species interactions involving invertebrates. One well-studied example is plant-invertebrate interactions. Shifts in temperature decouple phenology of flowering and invertebrate emergence, potentially reducing pollination Memmott *et al*. (2007) and herbivory. Increased atmospheric CO_2 concentrations could also affect plant C:N ratios for many plant species (Ayres, 1993; Zvereva & Kozlov, 2006), consequently altering food quality for herbivores and detritivores. Changes in plant quality due to climate change can lead to altered growth, survival, and/or feeding rates in herbivorous and detritivorous invertebrates in aquatic and terrestrial environments (Roth & Lindroth, 1994; Hughes & Bazzaz, 2001; Tuchman *et al*., 2002; Zvereva & Kozlov, 2006). Variations in plant quality and other traits can affect the ability of invertebrates associated with plants to find adequate resources, influencing invertebrate population size, life history traits, and behavior, all of which may affect invertebrate impacts on ecosystem services.

While much of the literature has examined plant – insect herbivore responses to climate change, altered interactions among competitors, parasites, pathogens, predators, and mutualists are also important (Tylianakis *et al*., 2008; Van der Putten, Macel & Visser, 2010). For example, increasing temperatures may alter interactions between marine amphipods and trematode parasites, leading to a collapse in amphipod populations (Mouritsen *et al*., 2005). Species range shifts will lead to different combinations of species, creating new biotic interactions that alter population dynamics of invertebrates, potentially altering invertebrate influences on ecosystem services.

Climate change affects invertebrates at all levels of ecological hierarchy (Table 3). At the level of the individual, physiological and behavioral responses to temperature change include phenological changes in emergence, development and migration, as well as changes in the timing and amount of resource consumption and reproduction (Bale *et al*., 2002). Consequently, individuals' responses to climate change cause shifts in population phenology, abundance, geographic distribution and genetics (Thomas *et al*., 2001; Parmesan & Yohe, 2003; Parmesan, 2006; Braune *et al*., 2008). Additionally, in some cases (e.g., butterflies and intertidal communities) entire communities characteristic of lower elevations and latitudes have shifted higher in elevation or poleward to match temperature change (Barry *et al*., 1995; Sagarin *et al*., 1999; Menendez *et al*., 2006; Wilson *et al*., 2007).

IV. INVERTEBRATES AFFECT A VAST ARRAY OF ECOSYSTEM SERVICES

As well as being highly responsive to climate change, invertebrates affect most all ecosystem services. We categorize ecosystem services, following the framework provided by the Millennium Ecosystem Assessment (WRI, 2003), as supporting, provisioning, regulating, and cultural

Table 3. Invertebrate characteristics that may make them particularly vulnerable to global climate change

Trait affected by climate change	Reason vulnerable	Example	References
Individual Physiology	Poor ability to cope with temperature change	Articulated brachiopods, with slow growth and metabolic rates, may be less tolerant of ocean temperature increase than other species because of their inability to raise metabolic rates (i.e., increase O_2 consumption) to cope with increased costs of elevated body temperature.	Peck (2008)
	Narrow thermal tolerance	The combined effects of warming and elevated CO_2 (and associated acidification) may cause the narrowing of the thermal tolerance range for some marine invertebrate species [e.g., the edible crab (*Cancer pagurus*)], with implications for species distributions and species interactions.	Metzger *et al*. (2007) and Portner (2008)
		Increased temperature in the tropics may have strong negative effects on invertebrate diversity (e.g., insects) because species adapted to the relatively stable, tropical climate have narrow thermal tolerance windows. Invertebrates in temperate areas that are already at their northward or upward range limits might lack thermal refuges.	Deutsch *et al*. (2008)
	Narrow moisture tolerance	Terrestrial soil invertebrates that experience stressful conditions (e.g., impacted by pollutants) may be less capable of tolerating extreme drought events.	Hojer *et al*. (2001)
	Narrow tolerance for associated environmental factor	Skeleton formation of benthic calcifers (corals, foraminifera, bryozoans, crustaceans, molluscs, echinoderms, etc.) may be impeded by acidification.	Raven *et al*. (2005)
		Reduced salinity from increased storm runoff can kill near-shore marine invertebrates.	Reviewed in Przeslawski *et al*. (2008)
	Subjected to multiple stressors	Marine and freshwater invertebrates are subjected to pollution, coastal runoff, increased turbidity, increased storm intensity, reduced salinity, acidification, etc. in addition to increased sea temperature.	Hutchings *et al*. (2007) and Przeslawski *et al*. (2008)
Population Density	Low fecundity/slower population growth	Red gorgonian *Paramuricea clavata* is at highextinction risk in the face of rapid change because it is long-lived but slow-growing.	Linares *et al*. (2007)
	Low abundance/rare		
	Longer generation time	Some marine bivalves and lobsters may take years to reach sexual maturity; species with longer generation times are slower to respond to environmental change.	Bianchini, Stephano & Ragonese (1998)
Distribution	Dispersal strategies/sessile	Many marine invertebrates are dependent upon ocean currents for larval dispersal (Levin, 2006); collapse of ocean currents could impede dispersal and recruitment in these species.	Reviewed in Przeslawski *et al*. (2008)
		Sessile and slow-moving benthic invertebrates (e.g. tunicates), as well as asexually reproducing colonial individuals, are unable to rapidly shift ranges to escape unfavorable conditions.	Petersen & Svane (1995) and Przeslawski *et al*. (2008)
	Range shifts (spatial mismatch with other species)	Different temperature preferences of insect parasitoids and their hosts could lead to spatial/temporal mismatches between them.	Hance *et al*. (2007)
	Contracting biomes	Intertidal and near-shore invertebrate habitat (i.e. seagrass beds, mangroves, reefs) may be unable to shift inward against man-made and natural barriers as sea-levels rise. Invertebrates in temperate areas that are already at their northward or upward range limits might lack thermal refugees.	Galbraith *et al*. (2002), Lovelock & Ellison (2007) and Waycott *et al*. (2007)

Table 3. Continued

Trait affected by climate change	Reason vulnerable	Example	References
	Restricted range (vs. widespread species)	Corals dependent upon a combination of light intensity (i.e. depth) and temperature will be unable to greatly shift ranges in response to increasing water temperatures.	Walther *et al*. (2000)
		Because brachiopods require hard substrates, which are less geographically widespread than soft substrates, they may be dispersal limited due to lack of suitable colonization sites.	Peck (2008)
Natural history traits	Food quality	Food quality (N content of leaves) for terrestrial and freshwater invertebrate herbivores decreases in carbon enriched atmospheres.	Coley (1998)
	Long recovery time after disturbance	More frequent and severe storm events will decrease time for recovery between major disturbances, preventing populations of coral and intertidal invertebrates from rebounding after being damaged or dislodged in storms.	Hutchings *et al*. (2007) and Przeslawski *et al*. (2008)
	Climate-related breeding requirements	Reduced area of Antarctic sea ice and associated ice algae results in reduced krill recruitment and abundance.	Loeb *et al*. (1997)
		Rising sea temperatures will decouple temperature and photoperiod cues, disrupting reproduction of many marine invertebrates.	Lawrence & Soame (2004)
	Specialist (narrow range of resources used)	Extreme weather events, predicted to increase in frequency and intensity with climate change, may disproportionately impact specialist herbivores [e.g., blue butterflies (*Cupido minimus*)] when host plants decline in response to changing conditions.	Piessens *et al*. (2009)
Adaptive ability	Low genetic variation w/in population	Calcifying benthic invertebrates may have limited ability to adapt to increasing ocean pH.	Przeslawski *et al*. (2008)
		Lotic invertebrates are often grouped into genetically distinct subpopulations locally adapted to conditions, and may have limited genetic variability for adaptation.	Hogg & Williams (1996)
Community			
Species composition	Low functional redundancy	Benthic invertebrate communities that lack functional redundancy may be especially sensitive to anthropogenic stressors (e.g., metal pollutants in streams), and by extension, other forms of environmental change.	Carlisle & Clements (2005)
	Range shifts	Increased global temperatures lead to poleward shifts in species' geographic ranges for many (*n* = ˜22) European butterfly species.	Parmesan *et al*. (1999)
	Communities sensitive to change	Recent climate change has altered macroinvertebrate stream community structure.	Durance & Ormerod (2007)
Phenology	Temporal mismatch with other species	Changes in phenology as a result of climate change of invertebrate pollinators versus herbivores of a hypothetical plant species suggest differential community-level responses.	Fabina, Abbott & Gilman (2010)
		For marine taxa (e.g. clams) with temperature-dependent spawning cues and planktotrophic larvae, spawning can become decoupled from phytoplankton availability.	Philippart *et al*. (2003), Edwards & Richardson (2004) and Hutchings *et al*. (2007)
Species interactions	Mutualist/dependent on other species; specialists	Obligate associates of live corals may suffer if corals are restricted by depth and temperature requirements.	Przeslawski *et al*. (2008)
		Benthic invertebrates with photosynthetic symbionts are negatively impacted by increased turbidity resulting from increased storm intensity and frequency.	Elfwing *et al*. (2003) and Hutchings *et al*. (2007)
		Spider predation has temperature-mediated effects on grasshopper survivorship.	Logan, Wolensensky & Joern (2006)

References are found in online Appendix S2.

services; however, some categories were combined or expanded in accordance with the most recent literature (any changes are noted in the text). Where available, we quantify the monetary value of invertebrate contributions to these services (using dollar values from published literature adjusted to 2010 USD values). The definitions of each service, major ecosystems affected, and major invertebrate taxonomic groups providing these services are summarized in Table 4.

(1) Supporting services

Supporting services are necessary for the maintenance of all other ecosystem services. Discussions of supporting services typically focus on primary production. Here we expand primary production to include pollination and seed dispersal, which are important drivers of primary production, and soil formation to the broader, more-inclusive category of habitat formation, which includes drivers of habitat formation: bioturbation and bioerosion. Additionally, we added hydrologic flux as a supporting service.

(*a*) *Primary production*

Primary production is essential to ecosystems at local and global scales because it bridges solar and biological energy and affects material cycles (Field *et al.*, 1998; Jobbagy & Jackson, 2000). Ultimately, primary production provides humans with resources, including food and biofuel. Invertebrates positively and negatively affect primary production through direct and indirect interactions. Herbivorous and detritivorous invertebrates convert primary production into energy and resources that are critical to organisms from higher trophic levels or other subsystems of food webs (Hairston, Smith & Slobodkin, 1960; Polis & Strong, 1996). Studies have demonstrated the abilities of invertebrates to affect primary production in a variety of habitats. In terrestrial systems, supporting examples come from forests (Laakso & Setala, 1999), agricultural land (Isaacs *et al.*, 2009), grasslands (Belovsky & Slade, 2000; Leriche *et al.*, 2001), and marshes (Silliman & Bertness, 2002). In aquatic systems, examples have been found in rocky intertidal zones (Menge, 2000), pelagic communities (Hairston & Hairston, 1993), streams (Hill, Ryon & Schilling, 1995; Morin, Bourassa & Cattaneo, 2001), benthic communities (Covich, Palmer & Crowl, 1999), and coral reefs (Hay & Taylor, 1985).

Invertebrates accelerate primary production directly through pollination (Klein *et al.*, 2007) and seed dispersal (Brunet & Von Oheimb, 2002), and indirectly through trophic cascades (Schmitz, Hamback & Beckerman, 2000) and facilitation of nutrient cycling (Covich, Palmer & Crowl, 1999; Lavelle *et al.*, 2006). However, invertebrates can also reduce primary production directly through herbivory, especially in outbreaks (Carson & Root, 2000), and indirectly through specific trophic interactions, including predation (Wise *et al.*, 1999; Leriche *et al.*, 2001). Although particular characteristics of the processes described above most likely determine whether invertebrates accelerate or inhibit primary production (e.g., the abundance of predators), the degree of invertebrate impacts could be affected by many factors, such as biodiversity (Hooper *et al.*, 2005; Stachowicz, Bruno & Duffy, 2007), trophic structure and interactions (Hairston & Hairston, 1993; Werner & Peacor, 2003), invertebrate feeding preferences (Coll & Guershon, 2002; Ho & Pennings, 2008), bottom-up forces (Menge, 2000; Denno *et al.*, 2002), and geographic variation (Pennings *et al.*, 2009; Schemske *et al.*, 2009).

(*i*) *Pollination.* Roughly three fourths of all plants and one third of all crops by volume are pollinator-dependent to some degree (Berenbaum *et al.*, 2007; Klein *et al.*, 2007). Insects provide most of the animal pollination in natural and agricultural systems globally (Klein *et al.*, 2007; Allsopp, de Lange & Veldtman, 2008). In unmanaged habitats, pollination facilitates primary production that supports entire ecosystems (Allen-Wardell *et al.*, 1998). Insufficient pollination may make plant species more vulnerable to extinction (Berenbaum *et al.*, 2007) by reducing fecundity (Burd, 1994), seed and fruit set, and genetic variability. In agricultural systems, invertebrate pollinators are responsible for successful production of most vegetables, fruits, nuts, seeds, and forage crops that sustain dairy and livestock production (Southwick & Southwick, 1992; Berenbaum *et al.*, 2007). Pollinator scarcity can lead to increased production costs by reducing crop yield and quality (Gallai *et al.*, 2009) or even total crop failure (Allen-Wardell *et al.*, 1998). Invertebrate pollinators consist largely of insects, especially wild and managed bees (Buchman & Nabhan, 1996; Allen-Wardell *et al.*, 1998; Berenbaum *et al.*, 2007; Klein *et al.*, 2007; Allsopp *et al.*, 2008).

The economic value of invertebrate crop pollination in the U.S. is estimated at \$3.66 billion/year (2010 USD) for unmanaged, native pollinators (Losey & Vaughan, 2006), and \$3.7–\$13 billion/year (2010 USD) for the European honeybee (Southwick & Southwick, 1992). These values, based on commercial production, are probably underestimates because they do not consider the multibillion-dollar value of home garden and natural vegetation pollination to property owners or outdoor enthusiasts (Southwick & Southwick, 1992; Allsopp *et al.*, 2008). However, predacious or parasitic invertebrates can also reduce invertebrate pollination services, as in the case of *Apis mellifera* (honey bee) declines due to mite infestations.

(*ii*) *Seed dispersal.* Seed dispersal by invertebrates reduces plant parent-offspring competition and links habitats spatially and temporally (Lundberg & Moberg, 2003; Kremen *et al.*, 2007). In general, invertebrates move seeds short distances (< 10 m for some ant species) compared to dispersal by vertebrates or wind (> 10 km; Corlett, 2009). The interaction of seeds and invertebrates spans a gradient from accidental encounters to highly co-evolved mutualisms. The latter include an estimated 11000 species of myrmecochores (Lengyel *et al.*, 2009), plants that attract ants with a lipid-rich food body and rely on ants as their primary dispersal agent (Giladi, 2006).

Table 4. Major ecosystem services that invertebrates provide or influence

Type of service	Ecosystem service	Definition of service	Major functional groups / key taxa	Affected ecosystems	Provide, influence, both
Supporting	Primary production	Biomass produced via photosynthesis	All trophic groups	Terrestrial: forests, agriculture, grasslands, marshes. Aquatic: rocky intertidal zones, pelagic communities, streams, benthic communities, coral reefs	Influence
	Seed dispersal	Movement of seeds away from the parent plant	Terrestrial: ants, dung beetles, ground beetles, earthworms, slugs; estuarine: polychaete worms	Global: especially arid and semi-arid environments (granivorous ants are common); tropical forests and savannas (dung beetle diversity is high), and regions where myrmecochores are concentrated (e.g., temperate deciduous forests)	Provide
	Pollination	The transfer of pollen between male and female flower parts	Unmanaged insects (bees, butterflies, flies, moths, wasps, ants, and thrips); managed bees (European honey bee, *Apis mellifera*; leafcutter bees, *Megachile* spp.; mason bees, *Osmia* spp.; bumble bees, *Bombus* spp.;, and alkali bees, *Nomia* spp.)	Agricultural and unmanaged terrestrial ecosystems globally	Provide
	Decomposition	The breakdown of detritus into its constituent nutrients	Aquatic: stoneflies (Plecoptera), caddisflies (Trichoptera), isopods, and amphipods. Marine: snails and crabs. Terrestrial: nematodes, annelids, and arthropods (e.g., Oribatid mites)	Global	Both
	Nutrient cycling	Movement of nutrients within and between ecosystems	Burrowing organisms (e.g. earthworms, marine lugworms), deposit feeders. Globally: herbivores, detritivores	Global	Both
	Hydrologic flux	Movement of water within and between ecosystems	Burrowing organisms, deposit feeders, terrestrial herbivores	Terrestrial, marine and freshwater sediments, terrestrial plants	Influence
	Habitat modification	Alteration of physical surroundings and/or changes the flow of resources	Colonial anemones, coral species, bivalves, caddisflies (Trichoptera), ants, termites, and earthworms, and other ecosystem engineers	Global	Provide

Table 4. Continued

Type of service	Ecosystem service	Definition of service	Major functional groups / key taxa	Affected ecosystems	Provide, influence, both
	Bio-turbation	Mixing and redistribution of sediment particles	Herbivores, omnivores, filter/suspension feeders, detritivores, crabs, mound-building termites, ants and earthworms (Lumbricidae and Megascolecidae)	Terrestrial, marine and freshwater sediments	Provide
	Bio-erosion	Biological breakdown of calcium carbonate rock via mechanical abrasion methods	Herbivores and detritivores (e.g., echinoids, gastropod molluscs, and chitons). Filter/suspension feeders (e.g., polychaetes, sipunculans, sponges, bivalves and barnacles)	Coral reefs, carbonate intertidal habitats, gastropod and bivalve shells, and deep sea, high latitude, and temperate substrates	Provide
Provisioning					
	Natural products	Goods obtained from natural ecosystems	Insects, shrimp, crabs, scallops, oysters, lobsters, corals, and many others	Natural and farmed marine, freshwater and terrestrial systems	Both
Regulating					
	Water quality	Filtering of particles and contaminants from water	Bivalves (i.e. mussels and oysters) and other groups	Freshwater and marine systems	Provide
	Food web stability	Reduction of fluctuation in community structure or interaction strengths	All trophic groups	Global, especially in species rich habitats	Both
	Disease regulation	The spread of diseases caused by invertebrates or spread by invertebrate vectors	For diseases that strongly impact humans: Diptera, Helminthes, ticks	Tropics, forests, and freshwater	Both
	Pest/invader control	The use of living organisms to suppress pests and reduce pest damage	Pest insect control: predatory and parasitic insects in the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Neuroptera; nematodes (particularly Steinernematidae, Heterorhabditidae and Mermithidae), mites, and spiders	Field crops, orchards, greenhouse and ornamentals, turf grass, vineyards, gardens; forests, grasslands, aquatic habitats	Provide
Cultural					
	Recreation services	The opportunity for recreational activities	All	Global	Both

Ants are likely the most conspicuous, well studied, and perhaps most common invertebrate seed dispersers. They range from the seed-harvesting, granivorous species (e.g., *Pogonomyrmex* spp.), to more generalist species that encounter and move seeds by accident. Dung beetles are also considered important secondary seed dispersers, transporting seeds in mammal dung horizontally to sites on the surface, or vertically to nutrient-rich sites below ground (Nichols *et al.*, 2008). Ground beetles, although less effective, may also disperse seeds (Ohkawara, Higashi & Ohara, 1996). Among non-insect invertebrates, terrestrial slugs (Turke *et al.*, 2010) and annelids in both terrestrial (Willems & Huijsmans, 1994; Eisenhauer *et al.*, 2008; Regnier *et al.*, 2008) and aquatic environments (Luckenbach & Orth, 1999) may be relatively important seed dispersers. Invertebrates that provide dispersal services are distributed worldwide but may be most influential in arid and semi-arid environments where granivorous ants are common (Willems & Huijsmans, 1994; Eisenhauer *et al.*, 2008; Regnier *et al.*, 2008), in tropical forests and savannahs where dung beetle diversity is greatest (Nichols *et al.*, 2008), and regions where myrmecochores are concentrated (e.g., temperate deciduous forests: Giladi, 2006).

Seed dispersal directly affects plant community organization and ecosystem services, such as food production. For example, invertebrates may facilitate the spread of exotics causing reduced production in agricultural systems [e.g., earthworms and giant ragweed (*Ambrosia trifida*); Regnier *et al.*, 2008]. Additionally, seed movement redistributes organic matter both horizontally and vertically, affecting nutrient cycling and decomposition rates (MacMahon, Mull & Crist, 2000; Nichols *et al.*, 2008). Consequently, some species of seed-harvesting ants have been used as biological indicators to assess ecosystem integrity (Underwood & Fisher, 2006).

(*b*) *Decomposition*

Most primary production eventually enters detrital food webs (Cebrian, 1999), where invertebrates are the dominant consumers (Seastedt, 1984; Mann, 1988; Wallace & Webster, 1996). Invertebrate detritivores fragment detritus into fine particles, easily used by microorganisms (Swift, Heal & Anderson, 1979), and produce frass, which increase detrital nutrient quality (Belovsky & Slade, 2000). Invertebrates also foster decomposition by dispersing fungal and bacterial propagules throughout the litter layer (Behan & Hill, 1978). Invertebrate-mediated decomposition also supports secondary production and enhances the formation of soil and aquatic sediments, maintaining ecosystem structure and function in benthic (freshwater and marine) and detritus-based food webs (Covich, Palmer & Crowl, 1999; Wall & Moore, 1999). Invertebrates mediate effects of detrital heterogeneity on decomposition (Hattenschwiler & Gasser, 2005; Swan & Palmer, 2006), and the top-down effects of invertebrate diversity on decomposition are stronger than the bottom-up effects of detrital diversity (Srivastava *et al.*, 2009). Herbivorous invertebrates may increase or decrease decomposition and nutrient release from litter, depending on the nutrient content and quality of preferred foliage (reviewed in Weisser & Siemann, 2004).

Invertebrate detritivores are commonly used as biological indicators among environmental management practices that help maintain organic matter processing (Lavelle *et al.*, 2006). The economic value (in 2010 US dollars) of dung beetles that actively decompose cattle feces in pasture and rangelands is estimated at $454 million (Losey & Vaughan, 2006). This waste would otherwise foul watersheds with heavy waste loads, affecting cattle production and water quality. On the other hand, invasive invertebrate decomposers may negatively impact ecosystems. For example, widespread invasions of exotic earthworms have reduced standing stocks of detritus in North American forests (Hendrix & Bohlen, 2002).

(*c*) *Nutrient cycling*

Invertebrates can redistribute and alter nutrient availability within an ecosystem through consumption and egestion of plants and detritus, and by physically moving materials and disturbing sediments via bioturbation and bioerosion. Selective feeding on vegetation, litter, or particulate organic matter (POM) may alter producer composition and POM quantity and quality, which in turn may either increase or decrease decomposition rates and nutrient availability in ecosystems. Invertebrate consumers transform organic matter into frass, the quality and internal porosity of which can stimulate or reduce nutrient transformation rates (Derouard *et al.*, 1997). In freshwater and marine systems, filter feeders remove POM and redistribute nutrients within the water column (Covich, Palmer & Crowl, 1999). Phloem-feeding invertebrates (Hemipterans) can also stimulate soil and microbial processes by producing highly labile honeydew (Dighton, 1978; Stadler, Muller & Orwig, 2006). However, honeydew may provide nutrients for colonizing foliar pathogens, thereby decreasing the ability of leaves to acquire energy (Blakeman & Fokkema, 1982), ultimately decreasing rates of primary production.

Invertebrates also impact the spatial distribution of nutrients between ecosystems. They redistribute nutrients from one system to another during outbreaks and emergence events (Yang, 2004; Yang *et al.*, 2008). For example, large-scale defoliations transfer nutrients from plant canopies to the litter surface, increasing ion export to streams (Swank *et al.*, 1981), and aquatic insect emergences redistribute nutrients from freshwater systems to terrestrial systems (Jackson & Fisher, 1986). Also, cyclic cicada emergences cause large nongaseous nitrogen fluxes from the soil to plants and litter (Callaham *et al.*, 2000; Yang, 2004).

(*d*) *Hydrologic flux*

Invertebrates influence water movement within and between ecosystems. Within ecosystems, detritivores decrease litter quantity (Wardle 2002) and burrowing soil invertebrates (e.g., earthworms) increase soil porosity (Derouard *et al.*, 1997), both of which enhance infiltration rates. Conversely, invertebrates with compact frass decrease soil porosity and infiltration rates (Swift, Heal & Anderson, 1979; Chauvel *et al*., 1999). Invertebrate herbivores increase plant water loss by damaging plant tissues, and allow more precipitation to reach the ground by decreasing canopy cover (reviewed in Schowalter, 2011). Similarly, benthic organisms in both freshwater and marine systems, especially burrowing organisms or deposit-feeding organisms, can increase porewater turnover (irrigation) and increase water in sediments, blurring the boundary layer between water and sediment (Rhoads & Young, 1970). In marine systems, larger burrowing organisms, such as large polycheate worms (*Nereis*) and lugworms (*Arenicola*), may especially increase porewater exchange in shallow coastal sediments (Kristensen & Blackburn, 1987).

Invertebrates also alter hydrologic flux between ecosystems. For example, the roots of invasive *Tamarix* spp. in the North American Southwest tap into ground and surface water, lowering water table levels and stream flow (Stromberg *et al*., 2007). Terrestrial biocontrol insects may counteract this hydrologic change by decreasing *Tamarix* abundance, restoring water table levels and streamflow rates (Shafroth *et al*., 2005).

(*e*) *Habitat formation and modification*

Many invertebrates are 'ecosystem engineers' (*sensu* Jones, Lawton & Shachak, 1994), i.e., organisms whose presence or activity alters their physical surroundings or changes resource flow, thereby modifying or creating habitats and influencing associated species (Jones, Lawton & Shachak, 1994; Crain & Bertness, 2006). These habitat changes range from local to biogeographic-scale modifications (Crain & Bertness, 2006), and help to maintain biodiversity, nutrient and biogeochemical cycles, and physical environments. For example, reef-building coral species form three-dimensional structures that serve as habitat for most coastal fish species (Luckhurst & Luckhurst, 1978) and protect coastal communities from strong ocean currents. Colonial anemones (*Coryanctis californica*) also create habitat for many macroalgal and invertebrate species (Levenbach, 2008). In aquatic habitats, bivalves and caddisflies directly produce and maintain biogenic substrates, providing stable habitat for other aquatic species (reviewed in Moore, 2006). In terrestrial systems, nesting structures built by ants, termites and earthworms promote soil formation, alter decomposition rates and indirectly promote biogeochemical cycling (Jouquet *et al*., 2006; Lavelle *et al*., 2006). Additionally, invertebrate ecosystem engineers have been used as bioremediators. For example, earthworms play a critical role in the removal of hydrocarbons from contaminated soils (Ceccanti *et al*., 2006). However, habitat modifications by invertebrates sometimes result in ecosystem disservices. For example, several bark beetle species increase tree mortality, modifying the physical attributes of temperate forests and negatively impacting the forestry industry (Bentz *et al*., 2009).

(*i*) *Bioturbation.* Bioturbation is the mixing and redistribution of sediments. Invertebrate burrowing, feeding, ventilatory, and locomotory behavior cause bioturbation, and these sediment-working techniques directly affect sediment structure and composition in terrestrial and aquatic environments (Murray, Meadows & Meadows, 2002; Meysman, Middelburg & Heip, 2006). For example, mucous-caused particle aggregation and size-selective particle feeding by invertebrates can homogenize or stratify distributions of sediment particle size. Additionally, vertical movement of material distributes organic matter within sediments and alters the distribution of dormant life history stages of planktonic organisms (Marcus & Schmidt-Gengenbach, 1986). Though individual invertebrate bioturbators displace sediment particles over spatial scales of only micrometers to decimeters, they can affect sediment geomorphology on the scale of meters to kilometers (Murray, Meadows & Meadows, 2002).

Invertebrate bioturbators can indirectly positively or negatively affect primary production (Thompson *et al*., 1993; Kristensen & Alongi, 2006) and influence hydrology and nutrient and gas fluxes by modulating water flow (Volkenborn *et al*., 2007) in both terrestrial (Richards, 2009) and aquatic ecosystems (Aller, 2001). Increased sediment surface area and bioirrigation enhance oxygen flux and aerobic microbial processes, including mineralization and respiration (Kristensen, 1988; Reichardt, 1988). Additionally, bioturbators can influence cycling rates of macro- and micronutrients (Kristensen & Blackburn, 1987; Magni & Montani, 2006). By altering various sediment properties, invertebrate bioturbators generate habitat complexity and influence community composition. However, sediment-destabilizing species (e.g., lugworms) can inhibit recruitment and establishment sessile epifauna, thereby reducing benthic diversity (Widdicombe *et al*., 2000).

(*ii*) *Bioerosion.* Bioerosion is the biological breakdown of carbonate rock into smaller fragments by mechanical abrasion and chemical dissolution of $CaCO_3$ (Neumann, 1966). Invertebrates bioerode carbonate substrata in terrestrial, aquatic and marine ecosystems by grazing and boring. Grazers, such as echinoids, scrape carbonate rock to consume algae, creating $CaCO_3$ chips, and etch cavities in substrates, often by chemical means, while macroborers, such as sponges, excavate chambers within carbonate substrate, using acid to soften the rock and then mechanically removing $CaCO_3$ chips (Hutchings, 1986). Invertebrate grazing and boring enhance species diversity by increasing available surface area for colonization (Hutchings, 1986; Pinn *et al*., 2008) and shelter for cryptofaunal communities. The balance between bioerosion and accretionary processes determines the structural integrity of carbonate substrata ecosystems, particularly coral reef environments (Hutchings, 1986). Bioerosion rates could be used to assess marine ecosystem health Holmes, Ortiz & Schonberg (2009) because negative net carbonate erosion results in the loss of carbonate substrata ecosystems (Reaka-Kudla, Feingold & Glynn, 1996).

(2) Provisioning services

Provisioning services are goods obtained from ecosystems. Humans use invertebrate products for food, clothing, medical treatments and building materials. Here, we focus on provisioning services produced directly by invertebrates, although invertebrates indirectly affect the production of many other products both positively and negatively. For example, crop pests negatively impact food production, but allow for the establishment of a multi-billion dollar pesticide industry. Collectively, goods provided by invertebrates comprise a multi-billion dollar industry and improve human quality of life.

(*a*) *Natural products*

(*i*) *Food*. Many invertebrates, including crustaceans and mollusks, are farmed and consumed globally. Some invertebrates are used as food for aquaculture, like the brine shrimp fed to farmed prawn and fish. Insects, with high protein and caloric content, comprise a large proportion of some human diets (Dufour, 1987; Meyers, 1997). In addition, other invertebrates, including jellyfish and tarantulas, are regarded as delicacies. Humans also consume products made by invertebrates, such as honey.

(*ii*) *Household goods and ornamental resources*. Invertebrates supply many common household goods. Silk is extracted from silkworm (*Bombyx mori*) cocoons. Scale insect secretions are used to produce shellac, a food glaze and wood finish, and cochineal, the ‘natural red 4’ dye used in cosmetics and paints. Marine sponges are used for various applications, including household cleaning and helmet lining. Corals and other marine invertebrates produce calcium carbonate, which is used for construction materials. Amberized mosquitoes and fossilized trilobites are used in jewelry, and other invertebrates create expensive ornamental products including pearls and red coral. Additionally, corals are also in high demand in the aquarium trade, an estimated $41–82 million (2010 USD) industry in the mid-1980s (Spurgeon, 1992). However, invertebrates can exact tremendous damage to household goods, such as caterpillars of the clothing moth (*Tineola bissellela*) that destroy fabric, or dermestid beetles that consume natural fibers, such as wool, silk, fur and feathers.

(*iii*) *Biochemicals and pharmaceuticals*. Insects secrete hormones and substances used in birth-control hormones, wound-healing promoters, antiviral agents, and cardiotonic factors (Eisner, 1992). Sea urchins contain holothurin, which is used to treat coronary disorders and cancer. Octopuses produce a compound that eases hypertension. Sponges have antiviral properties that suppress the common cold. Chitin from crustacean skeletons cures fungal infections, heals wounds, and kills malignant cells. Barnacles possess a compound potentially useful for tooth and bone fillings (Meyers, 1997). However, some invertebrates, through harmful stings and bites, create a need for the development and use of biochemicals and pharmaceuticals. For example, life-saving antivenom is extracted from several species of scorpions, spiders, ticks, and jellyfish.

(*iv*) *Genetic resources*. Humans use genetic resources, the hereditary material of species, to identify and maintain ecologically important strains of organisms. The U.S. Department of Agriculture National Invertebrate Genetic Resources Program (http://www.ars-grin.gov/nigrp/index.html) maintains stocks of pollinators, biocontrol agents, disease-resistant strains and reference specimens of pest invertebrates. For example, this program identified a honeybee strain that is resistant to the invasive mites that have destroyed U.S. bee populations.

(3) Regulating services

Regulating services are those that regulate ecosystem processes or maintain ecosystem structure. We focus on how invertebrates affect water quality, stabilize food webs, and help regulate diseases and pests/invaders. Additional regulating services are described in other sections (e.g., erosion control and storm protection in the section on habitat modification).

(*a*) *Water quality*

Invertebrate filtering of particles and contaminants from water counters eutrophication and pollution. In shallow marine and freshwater ecosystems, bivalves (i.e., mussels and oysters) often comprise most invertebrate biomass and filter 10–100% of the water column, though insects and other invertebrates also contribute (Strayer *et al*., 1999). By transferring energy and nutrients from the water column to the benthos, bivalves can remove pelagic and drifting contaminants and help reduce toxic phytoplankton blooms.

Invertebrates and their diversity are important biological indicators of water quality (Lenat, 1988). The presence or absence of particular taxa is used in bioassessment protocols to examine habitat heterogeneity and water quality in aquatic ecosystems (Barbour *et al*., 1999). However, water quality maintenance often requires diverse assemblages of bivalves with unique and complimentary traits (Caraco *et al*., 2006; Spooner & Vaughn, 2008); therefore, restoring native invertebrate populations may not be sufficient to re-establish their ability to adequately maintain healthy water quality because anthropogenic environmental changes place invertebrate communities at risk (Pomeroy, D’Elia & Schaffner, 2006; Spooner & Vaughn, 2006, 2008; Coen *et al*., 2007). In the case of the invasive zebra mussel (*Dreissena polymorpha*), excessive water filtration has altered the Great Lakes, greatly reducing plankton levels, shifting these food webs from predominantly pelagic to benthic (bottom-feeding), and increasing water clarity.

(*b*) *Food web stability*

The high taxonomic diversity and biomass of invertebrates helps to reduce fluctuations in the community composition and intensity of interactions within food webs. Increased species richness may generate sufficient functional redundancy to buffer against perturbations (Naeem, 1998). Even in simple food webs, the addition of invertebrate consumers can dramatically alter relationships between biodiversity and rates of ecosystem processes, such as productivity, or between biodiversity and community stability (Worm & Duffy, 2003). Examples of invertebrate effects on community stability are common (e.g., richness of sessile animals is associated with increased resistance and resilience of marine communities with respect to disturbance or invasion (Stachowicz, Bruno & Duffy, 2007). However, invertebrate organisms can also be the cause of destabilizing food web ecosystems, especially in the case of invasive invertebrates (Dick, Platvoet & Kelly, 2002; McNickle, Rennie & Sprules, 2006). Even when an invasion is relatively benign, the invader may facilitate invasion by additional species, thereby accelerating changes in biodiversity and community structure (Simberloff & Von Holle, 1999; Grosholz, 2005).

Maintenance of food web stability can be either top-down or bottom-up. In rocky intertidal communities, invertebrate predators reduce the intensity of competition among other species (e.g., Connell, 1961), thereby forestalling competitive exclusion and maintaining high biodiversity (Paine, 1969). Invertebrate predators and parasites may also regulate prey populations, indirectly affecting services provided by these species. In addition, parasitism is among the most prevalent trophic interactions and increases connectivity within food webs, increasing their stability (Lafferty, Dobson & Kuris, 2006*a*; Lafferty *et al*., 2006*b*).

Conversely, invertebrate prey species provide important resource subsidies to consumers and link terrestrial and aquatic food webs (Nakano & Murakami, 2001; Baxter, Fausch & Sanders, 2005). These subsidies directly and indirectly affect food web structure by substantially affecting predator energy budgets, abundance, growth, and behavior (Baxter, Fausch & Sanders, 2005). In addition, invertebrates influence resource availability to other consumers, for example, by altering detrital characteristics in processing chains (e.g., Covich, Palmer & Crowl, 1999).

(*c*) *Disease regulation*

Invertebrates serve as hosts for countless parasites and pathogens (Poulin & Morand, 2000); conversely, invertebrate predators and parasitoids also regulate many parasites and disease vectors. As the number of invertebrate species is still unknown, the number of pathogens and parasites that use invertebrates as hosts is also unknown (Poulin & Morand, 2000). Nevertheless, pathogens and parasites are important ecosystem components that regulate host populations and species interactions (Marcogliese & Cone, 1997; Mouritsen & Poulin, 2002; Hatcher, Dick & Dunn, 2006).

Many infectious human diseases are transmitted by invertebrate vectors, including Lyme disease (ticks) and West Nile Virus (mosquitoes) (Pongsiri *et al*., 2009). Nine of the 13 priority diseases identified by the Special Programme for Research and Training in Tropical Diseases are either transmitted by invertebrate vectors (e.g. malaria, dengue, onchocerciasis), use invertebrates as hosts (schistosomiasis), or are caused by invertebrates (e.g. helminthes, schistosomiasis) (http://apps.who.int/tdr/svc/diseases). An estimated 520 million people in the tropics are infected annually with diseases borne by invertebrate vectors and about 200 million more people are infected with diseases that use invertebrates as intermediate hosts (Hay, Packer & Rogers, 1997). Many of these diseases have serious social and economic costs. Malaria, for example, kills more than 1 million people annually and exacts considerable economic costs including medical costs and lost income (Sachs & Malaney, 2002). However, many invertebrates also control invertebrate vectors of disease. For example, a variety of arthropods prey on ticks in nature, including nematodes, spiders, mites, predatory hemipterans and ants (Samish & Rehacek, 1999). Additionally, many invertebrate natural enemies are being developed for vector control. *Notonecta* sp., predatory copepods, and predatory *Toxorhynchites* mosquitoes have been successfully used in field trials for inundative biocontrol of mosquito disease vectors (Lacey & Orr, 1994) and copepods in particular show potential for controlling mosquitoes in artificial containers such as those found around human habitations (Rey *et al*., 2004). Schistosomiasis, caused by parasitic flatworms that use snails as intermediate hosts, can be controlled by trematode parasites or snail species that compete with host snail populations (Pointier & Jourdane, 2000).

(*d*) *Pest/invader control*

Biocontrol is the use of organisms to reduce the abundance of pest populations and thus decrease pest damage. Invertebrates control crop-feeding insects and disease vectors through parasitism, direct predation, or transmission of viruses, bacteria and toxins (Hajek, 2004). Invertebrates can also disrupt biocontrol through intraguild predation (Polis, Myers & Holt, 1989). Insects control invasive weeds by consuming biomass, reducing reproductive output, and increasing plant susceptibility to other stressors (van Driesche & Bellows, 1996). Biocontrol of weeds is often most effective when multiple forms of herbivory are employed including direct feeding, mining, boring, and gall-forming. For example, the weevil *Cyrtobagous salviniae* can clear lakes of millions of tons of the aquatic weed *Salvinia molesta* because larvae tunnel through and feed on vascular tissue, while adults feed on meristems (Hajek, 2004). Biocontrol of disease vectors and agricultural pests are other examples of the important roles that some invertebrate consumers play in feeding on other invertebrate species (e.g., Yusa, 2006).

Biocontrol of native crop pests by native or naturalized insects is valued at \$5.4 billion annually (2010 USD) in the U.S. (Losey & Vaughan, 2006). However, this estimate excludes money saved through biocontrol of invasive crop pests, disease-spreading insects, and invasive weeds. This is an important omission because the value of naturally occurring biocontrol of a single invasive insect (the soybean aphid, *Aphis glycines*) in only four U.S. states was estimated between $256 and $1.5 billion/year in 2010 USD (Landis *et al.*, 2008).

(4) **Cultural services**

Cultural services are nonmaterial benefits obtained from ecosystems. Invertebrates provide many of these benefits, as they are spiritually and aesthetically valued in some cultures. However, the values of such services are not easily quantifiable, because cultural attitudes vary widely among individuals and communities. Support for conservation of invertebrates that mediate important ecosystem services will largely be driven by people's values and preferences. Here, we describe recreation services and briefly other cultural services.

(*a*) *Recreation services*

Recreational services are those that provide opportunities for recreational activities, e.g. outdoor activities, nature viewing such as bird watching, and eco-tourism. We can estimate the monetary value of invertebrates' contributions to recreational activities such as fishing, hunting, and wildlife-viewing following the methodology of Losey & Vaughan (2006) and using the current National Survey of Fishing, Hunting, and Wildlife-Associated Recreation (U.S. Department of the Interior *et al.*, 2006). We estimated this value at approximately $77 billion in total 2010 USD directly or indirectly supported by invertebrates (Table 5). Additionally, marine systems populated with invertebrates attract millions of tourists each year. Recreational diving is a multi-billion dollar global industry (Moberg & Folke, 1999). Coral reef communities generate $11.5 billion annually (2010 USD) from tourism and recreation (Cesar, Burke & Pet-Soede, 2003). Yet invertebrates also can hinder outdoor recreation; for example, groups of large Humbolt squid swam into shallow California waters in 2009, alarming swimmers and divers (Post/AP, Huffington, 2009). Unwelcomed mosquitoes, bees/wasps, ticks, flies, spiders, cockroaches and ants, can thwart other indoor or outdoor activities.

(*b*) *Other cultural services*

In addition to important material contributions, invertebrates entertain and stimulate people. In ancient times, scarab beetles (*Scarabaeus sacer*) were worshipped by Egyptians as symbols of the sun god and therefore were used in art and burial rituals. Currently, numerous insect zoos and museums allow visitors to observe and handle insects while learning about their biology and importance. Tours are available to see invertebrate phenomena such as Monarch butterfly migrations, glowworms, dung beetles, and dragonflies (Huntly, Van Noort & Hamer, 2005). Many people enjoy interacting with invertebrates by keeping ant farms, tarantula and scorpion pets, butterfly gardens and insect collections, to name a few. Many other invertebrates inspire modern art, music, a multi-billion dollar movie industry (Table 6), clothing and even car designs (e.g., Volkswagon beetle). A Google search for invertebrate-related activities and art ('insect art', 'invertebrate art') returned 1.5 million hits (June 2012), including an annual insect fear film festival (http://www.life.illinois.edu/entomology/egsa/ifff.html). Blogs with 'insect' themes or subject content also returned nearly 4 million hits.

Table 5. Outdoor recreation activities influenced by invertebrates

Activity	Participants	Proportion	TAR	ISR
Hunting	12.5	—	$27.34	—
Small game	4.8	0.51*	$2.86	$0.56
Migratory bird	2.3	0.43*	$1.55	$0.23
Fishing	30	—	$50.14	—
Freshwater	25.4	1	$31.40	$31.40
Wildlife watching	71.1	—	$54.55	—
Around home	67.8	—	—	—
Birding	41.8	0.61*	$32.11	$20.65
Insects/spiders	16	1	$13.13	$13.13
Away from home	23	—	—	—
Birding	20	0.61*	$15.16	$9.31
Other wildlife	10.4	1	$8.24	$8.24
Total recreation	87.5	—	$145.10	$83.51

The number of participants (in millions of people) and total activity revenue (TAR; in billions of U.S. dollars) were obtained from the National Survey of Fishing, Hunting, and Wildlife-Associated Recreation (U.S. Department of the Interior *et al.*, 2006). The proportion of wildlife influenced by invertebrates, denoted by (*) was determined by Losey & Vaughan (2006). Invertebrate-supported revenue (ISR; in billions of U.S. dollars) is the product of the total activity revenue and the proportion influenced by invertebrates.

V. FUTURE DIRECTIONS: CONSEQUENCES OF INVERTEBRATE RESPONSES TO CLIMATE CHANGE ON ECOSYSTEM SERVICES

As we demonstrate in Section II, there is a substantial lack of studies linking invertebrate responses to climate change to consequences for ecosystem services. There have indeed been some recently documented insect-mediated changes in ecosystem services under climate change (Volney & Fleming, 2000; Ladanyi & Horvath, 2010; Rojas, Locatelli & Billings, 2010, Moraal & Jagers Op Akkerhuis, 2011; Rafferty & Ives, 2011), but these are far and few between and tend to only be services (and disservices) directly provided by invertebrates, often ignoring the indirect effects through food web interactions (Traill *et al.*, 2010). Because they are known to be highly sensitive to climate change, the consequences of invertebrate responses to climate change for ecosystem services need to be evaluated. We present a simple decision tree showing the information needed to make a well-informed recommendation for how to manage invertebrates that influence vulnerable ecosystem services (Figure 3). These studies are still far too few to provide us with any general understanding of how the services provided by this important animal group are being/predicted to be altered under climate

Table 6. Invertebrate-related movie revenue, using data collected from www.boxofficemojo.com, reported in U.S. dollars (2010 USD), and only U.S. domestic revenue is denoted (*)

Movie title	Production company (release date)	Total gross (in millions USD)
Alien	Fox (May 1979)	$104.9
Antz	DreamWorks (October 1998)	$171.8
Arachnophobia	Buena Vista (July 1996)	$ 53.2*
Bee Movie	Paramount/ DreamWorks (November 2007)	$287.6
Bug	Paramount (June 1975)	$3.6
Bugs! (IMAX)	SK Films (March 2003)	$29.4
A Bug's Life	Buena Vista (November 1998)	$363.4
Eight Legged Freaks	Warner Bros. (July 2002)	$45.9
The Fly	Fox (August 1986)	$60.6
Joe's Apartment	Warner Bros. (July 1996)	$ 4.6*
Mimic	Miramax (August 1997)	$ 25.5*
Slither	Universal (May 2006)	$12.8

change. We suggest that land managers or others involved in making recommendations for how to conserve vulnerable ecosystem services could be substantially improved by interdisciplinary collaborations among invertebrate and ecosystem scientists, economists, sociologists and engineers (Figure 2). This figure also depicts at which steps members of an interdisciplinary team may provide the most input. Obviously, each step represents information that can indeed be hard and costly to obtain. Below, we make suggestions for how each group may go about obtaining the information they need, and how land managers may use this information to make informed decisions.

(1) Recommendations to scientists and other researchers

(*a*) *A call for invertebrate-mediated ecosystem services research*

We encourage scientists to undertake experiments that quantify the potential effects, whether positive or negative, of invertebrate effects on ecosystem services whenever possible, and where possible to look at climate change effects on these influences, in particular to inform steps 1–4 (Figure 2). Collaborations with between invertebrate and ecosystem scientists could facilitate appropriate measurements that invertebrate biologists have not traditionally used but that have been used extensively in microbial and plant systems (e.g., nutrient fluxes; Melillo *et al*., 2002). Improved employment of these tools can be facilitated through increased emphasis on ecosystem services when training undergraduate and graduate students working in invertebrate systems. Collaborations between invertebrate and ecosystem ecologists also could be initiated through organized workshops and working groups related to the interplay of global change, invertebrate responses and ecosystem services at regional and national scientific meetings. Particularly fruitful areas of research to improve conservation decisions may be to:

- Determine how invertebrates in producer and decomposer food webs mediate ecosystem services. This has been done for aquatic macroinvertebrates (Bady *et al*., 2005; Feld & Hering, 2007; Statzner, Bonada & Doledec, 2007; Carlisle *et al*., 2008; Doledec & Statzner, 2008) and herbivorous and predator invertebrates (Bell *et al*., 2008; Davis & Raghu, 2010; Hitchmough & Wagner, 2011).
- Determine how invasion or human-mediated relocation of invertebrates affects ecosystem processes and services. Identification of potential new invertebrate pests is also needed (Vanninen *et al*., 2011).
- Examine spatial and temporal patterns, functional and genetic components of invertebrate biodiversity that affect ecosystem services (Feld *et al*., 2009).

A variety of approaches should be used to determine how invertebrate responses to climatic change affect ecosystem services. For example, Gotelli, Ulrich & Maestre (2011) report randomization tests and software that can be used to determine species' importance in ecosystem function using natural variation in species' presence and ecosystem variables. These associations can then be validated by laboratory studies that manipulate invertebrate diversity and density and measure the resulting service of interest (e.g., nutrient flux, primary productivity, biomass for food production, etc.). Studies should also use field and laboratory addition/removal treatments of invertebrates, particularly in conjunction with alterations to abiotic variables expected to be altered by climate change (i.e., minimum, maximum, mean and variance in temperature or precipitation) and quantify responses of variables indicative of ecosystem services (e.g., plant productivity, water clarity, disease transmission, etc.). Studies also should consider the indirect effects of invertebrates on alterations to ecosystem processes and services, as well as climate feedbacks, through food web or other species interactions (Wallin & Raffa, 2001; Classen *et al*., 2005; Schowalter, 2011).

(*b*) *A call for interdisciplinary research*

In addition to gathering more empirical data on the linkages between invertebrates, climate change, and ecosystem services, management, and policy decisions will be better informed by efforts that include interdisciplinary collaborations. In particular, we suggest collaborations with: economists, who can provide better quantification of the economic value of invertebrate contributions to ecosystem services: sociologists, who can help improve the understanding of cultural value of invertebrates, and feasibility of management strategies for human populations; and with engineers who can develop and suggest better ways of managing invertebrates of physically supporting vulnerable ecosystem services. Strategies to initiate dialogue and collaboration among these groups may include:

- Recruitment of interdisciplinary teams through advertisements in listservs (e.g., envtecsoc, Environment, Technology and Society), journals (e.g., *Journal of Environmental Economics and Management*, *Ecology and Society*, or *Ecosystems*) and at conferences [e.g., The Association for Environmental Studies and Sciences (AESS)] associated with professionals working in economics, sociology, or other fields.
- Encouragement of funding solicitations for interdisciplinary collaboration from government and private organizations.
- Initiating intra-university projects that include principal investigators and students working in these various disciplines, e.g., through the National Science Foundation Integrative Graduate Education and Research Traineeship program.
- Planned future ecosystem assessments (like the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) should include input from interdisciplinary experts in order to better consider the effects of biodiversity, including explicitly invertebrates, on the sustainability of ecosystem services, as suggested in Figure 2.

(2) Recommendations for managers: a call for managers to implement results of empirical work

One of the major questions that managers struggle with in relation to this type of work is: *when should we intervene to conserve ecosystem services influenced by invertebrates?* We suggest that managers dealing with an ecosystem service that is heavily influenced by invertebrates work closely with scientists and other researchers to collect the information suggested in Figure 2. In particular:

- Conduct biomonitoring of invertebrate communities to monitor changes in invertebrate populations and communities over time. Managers should seek the help of invertebrate specialists and ecosystem scientists alike to decide what groups of invertebrate species to monitor. Understanding of which invertebrates to monitor in a particular ecosystem will have to be developed on a case-by-case basis depending on the service of interest and the system.
- Initiate informed discussions with stakeholders and policy makers.
- Increase public awareness of the role invertebrates play in ecosystem service management. Increased public awareness can be achieved by reaching out to local schools and park visitors as well as through radio and television appearances and journal, magazine and newspaper editorials (Primack, 1993).

VI. CONCLUSIONS

(1) In his classic paper 'The little things that run the world', E.O. Wilson (1987) claimed that human life could not persist beyond a few months if invertebrates disappeared. Here, we demonstrate that significant knowledge gaps exist in understanding how invertebrate effects on humans may be altered by climate change. Accordingly, we summarized how invertebrates, the dominant taxa in most ecosystems, affect almost all categories of ecosystem services and are also highly sensitive to climate change.

(2) To understand how to sustain ecosystem services for human societies, it is imperative to understand what organisms and mechanisms affect these services.

(3) Therefore, we argue that conservation efforts to mitigate effects of climate change on ecosystem services must include consideration of invertebrate populations. In particular, we suggest that interdisciplinary groups be used to collect necessary information to make informed decisions about when and how conservation efforts to manage for ecosystem services mediated by invertebrates should be accomplished.

VII. ACKNOWLEDGEMENTS

This paper is the result of a LTER working group and follow-up workshop, which was funded by the LTER LNO and approved by the LTER Executive Board. We thank members of our original working group at the 2009 LTER All Scientists meeting for interesting discussions, and the Harvard Forest staff for logistical support at our second working group. We also thank Elise Gornish, Rob Dunn, Alan Covich, Aimée Classen and Verónica Ferreira for reviewing earlier drafts of this manuscript.

VIII. REFERENCES

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P. A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C. E., Kennedy, K., Kevan, P., Koopowitz, H., et al. (1998). The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* **12**, 8–17.

Aller, R. C. (2001). Transport and reactions in the bioirrigated zone. In *The Benthic Boundary Layer: Transport Processes and Biogeochemistry* (eds B. P. Boudreau and B. B. Jorgensen), pp. 269–301. Oxford University Press, New York.

Allsopp, M. H., de Lange, W. J. & Veldtman, R. (2008). Valuing insect pollination services with cost replacement. *PLoS ONE* **3**, 8.

Ayres, M. P. (1993). Plant defense, herbivory and climate change. In *Biotic Interactions and Global Change* (eds J. G. K. P. Kareiva and R. B. Huey), pp. 75–94. Sinauer Associates Inc, Sunderland.

Bady, P., Doledec, S., Fesl, C., Gayraud, S., Bacchi, M. & Scholl, F. (2005). Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. *Freshwater Biology* **50**, 159–173.

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., et al. (2002). Herbivory in global climate cahnge research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**, 1–16.

Balmford, A., Rodrigues, A., Green, R., Fisher, B., Naidoo, R., Strassburg, B. & Turner, K. (2011). Bringing ecosystem services into the real world: an operational framework for assessing the economic consequences of loosing wild nature. *Environmental and Resource Economics* **48**, 161–175.

Barbour, M. T., Gerritsen, J., Snyder, B. D. & Stribling, J. B. (1999). *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates, and Fish*. U. S. Environmental Protection Agency, Office of Water, Washington.

Barry, J. P., Baxter, C. H., Sagarin, R. D. & Gilman, S. E. (1995). Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* **267**, 672–675.

Baxter, C. V., Fausch, K. D. & Sanders, W. C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* **50**, 201–220.

Behan, V. M. & Hill, S. B. (1978). Feeding-habits and spore dispersal of oribatid mites in the North American Arctic. *Revue d'Ecologie et de Biologie du Sol* **15**, 497–516.

Bell, J. R., Traugott, M., Sunderland, K. D., Skirvin, D. J., Mead, A., Kravar-Garde, L., Reynolds, K., Fenlon, J. S. & Symondson, W. O. C. (2008). Beneficial links for the control of aphids: the effects of compost applications on predators and prey. *Journal of Applied Ecology* **45**, 1266–1273.

Belovsky, G. E. & Slade, J. B. (2000). Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 14412–14417.

Bentz, B., Logan, J., MacMahon, J. & Allen, C. (2009). *Bark Beetle Outbreaks in Western North American: Causes and Consequences*. University of Utah Press, Chicago.

Berenbaum, M. R., Bernhardt, P., Buchmann, S., Calderone, N. W., Goldstein, P., Inouye, D. W., Kevan, P., Kremen, C., Medellin, R. A., Ricketts, T. H., Robinson, G. E., Snow, A. A., Swinton, S. M., Thein, L. B. & Thompson, F. C. (2007). *Status of Pollinators in North America*. The National Acadamies Press, Washington.

Blakeman, J. P. & Fokkema, N. J. (1982). Potential for biological control of plant diseases on the phylloplane. *Annual Review of Phytopathology* **20**, 167–192.

Boulton, A. J., Fenwick, G. D., Hancock, P. J. & Harvey, M. S. (2008). Biodiversity, functional roles and ecosystem services of groundwater invertebrates. *Invertebrate Systematics* **22**, 103–116.

Braune, E., Richter, O., Sondgerath, D. & Suhling, F. (2008). Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology*, **14**, 470–482.

Brunet, J. & Von Oheimb, G. (2002). Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* **86**, 429–438.

Brusca, R. C. & Brusca, G. J. (2002). Invertebrates. Second Edition. Sinauer Associates, Sunderland.

Buchman, S. L. & Nabhan, G. P. (1996). *The Forgotten Pollinators*. Island Press, Washington.

Burd, M. (1994). Bateman principle and plant reproduction – the role of pollen limitation in fruit and seed set. *The Botanical Review* **60**, 83–139.

Callaham, M. A., Whiles, M. R., Meyer, C. K., Brock, B. L. & Charlton, R. E. (2000). Feeding ecology and emergence production of annual cicadas (Homoptera : Cicadidae) in tallgrass prairie. *Oecologia* **123**, 535–542.

Caraco, N. F., Cole, J. J. & Strayer, D. L. (2006). Top-down control from the bottom: regulation of eutrophication in a large river by benthic grazing. *Limnology and Oceanography* **51**, 664–670.

Carlisle, D. M., Hawkins, C. P., Meador, M. R., Potapova, M. & Falcone, J. (2008). Biological assessments of Appalachian streams based on predictive models for fish, macroinvertebrate, and diatom assemblages. *Journal of the North American Benthological Society* **27**, 16–37.

Carpenter, S. R., Mooney, H. A., Agard, J., Capistrano, D., DeFries, R. S., Diaz, S., Dietz, T., Duraiappah, A. K., Oteng-Yeboah, A., Pereira, H. M., Perrings, C., Reid, W. V., Sarukhan, J., Scholes, R. J. & Whyte, A. (2009). Science for managing ecosystem services: beyond the millennium ecosystem assessment. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 1305–1312.

Carson, W. P. & Root, R. B. (2000). Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs* **70**, 73–99.

Cebrian, J. (1999). Patterns in the fate of production in plant communities. *American Naturalist* **154**, 449–468.

Ceccanti, B., Masciandaro, G., Garcia, C., Macci, C. & Doni, S. (2006). Soil bioremediation: combination of earthworms and compost for the ecological remediation of a hydrocarbon polluted soil. *Water, Air, and Soil Pollution* **177**, 383–397.

Cesar, H. J. S., Burke, L. & Pet-Soede, L. (2003). *The Economics of Worldwide Coral Reef Degradation*. Cesar Environmental Economics Consulting, WWF, Zeist, Arnhem.

Chan, K., Shaw, M., Cameron, D., Underwood, E. C. & Daily, G. C. (2006). Conservation planning for ecosystem services. *PLoS Biology* **4**, e379.

Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M. & Lavelle, P. (1999). Pasture damage by an Amazonian earthworm. *Nature* **398**, 32–33.

Classen, A. T., Hart, S. C., Whitham, T. G., Cobb, N. S. & Koch, G. W. (2005). Insect infestations linked to shifts in microclimate: important climate change implications. *Soil Science Society of America Journal* **69**, 2049–2057.

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P. & Tolley, S. G. (2007). Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* **341**, 303–307.

Coll, M. & Guershon, M. (2002). Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* **47**, 267–297.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthalamus stellatus*. *Ecology* **42**, 710–723.

Corlett, R. T. (2009). Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica* **41**, 592–598.

Covich, A. P., Palmer, M. A. & Crowl, T. A. (1999). The role of benthic invertebrate species in freshwater ecosystems. *Bioscience* **49**, 119–127.

Crain, C. M. & Bertness, M. D. (2006). Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* **56**, 211–218.

Davis, A. S. & Raghu, S. (2010). Weighing abiotic and biotic influences on weed seed predation. *Weed Research* **50**, 402–412.

Denno, R. F., Gratton, C., Peterson, M. A., Langellotto, G. A., Finke, D. L. & Huberty, A. F. (2002). Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* **83**, 1443–1458.

Derouard, L., Tondoh, J., Vilcosqui, L. & Lavelle, P. (1997). Effects of earthworm introduction on soil processes and plant growth. *Soil Biology and Biochemistry* **29**, 541–545.

Dick, J. T. A., Platvoet, D. & Kelly, D. W. (2002). Predatory impact of the freshwater invader Dikerogammarus villosus (Crustacea: Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1078–1084.

Dighton, J. (1978). Effects of synthetic lime aphid honeydew on populations of soil organisms. *Soil Biology and Biochemistry* **10**, 369–376.

Doledec, S. & Statzner, B. (2008). Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. *Freshwater Biology* **53**, 617–634.

van Driesche, R. G. & Bellows, T. S. Jr. (1996). *Biological Control*. Chapman & Hall, New York.

Dufour, D. L. (1987). Insects as food: a case study from the Northwest Amazon. *American Anthropologist* **89**, 383–397.

Dupont, S., Havenhand, J., Thorndyke, W., Peck, L. & Thorndyke, M. (2008). Near-future level of co2-driven ocean acidification radically affects larval survival and development in the brittlestar ophiothrix fragilis. *Marine Ecology Progress Series* **373**, 285–294.

Durance, I. & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology* **13**, 942–957.

Eisenhauer, N., Milcu, A., Sabais, A. C. W. & Scheu, S. (2008). Animal ecosystem engineers modulate the diversity-invasibility relationship. *PLoS ONE* **3**, 1–7.

Eisner, T. (1992). The hidden value of species diversity. *Bioscience* **42**, 578.

Elwood, M. F. & Foster, W. A. (2004). Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* **429**, 549–551.

Feld, C. K. & Hering, D. (2007). Community structure or function: effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology* **52**, 1380–1399.

Feld, C. K., da Silva, P. M., Sousa, J. P., de Bello, F., Bugter, R., Grandin, U., Hering, D., Lavorel, S., Mountford, O., Pardo, I., Partel, M., Rombke, J., Sandin, L., Jones, K. B. & Harrison, P. (2009). Indicators of biodiversity and ecosystem services: a synthesis across ecosystems and spatial scales. *Oikos* **118**, 1862–1871.

Field, C., Behrenfeld, M., Randerson, J. & Falkowski, P. (1998). Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**, 237–240.

Fischlin, A., Midgley, G. F., Price, J., Leemans, R., Gopal, B., Turley, C., Rounsevell, M., Dube, O., Tarazona, J. & Velichko, A. (2007). Ecosystems, their properties, goods, and services. In *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds O. C. M. Parry, J. Palutikof, P. van der Linden and C. Hanson), pp. 211–272. Cambridge University Press, Cambridge.

Gallai, N., Salles, J. M., Settele, J. & Vaissiere, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* **68**, 810–821.

Giladi, I. (2006). Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* **112**, 481–492.

Gotelli, N. J., Ulrich, W. & Maestre, F. T. (2011). Randomization tests for quantifying species importance to ecosystem function. *Methods in Ecology and Evolution* **2**, 634–642.

Grosholz, E. D. (2005). Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 1088–1091.

Hairston, N. J. & Hairston, N. S. (1993). Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* **142**, 379–411.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960). Community structure, population control, and competition. *American Naturalist* **94**, 421–425.

Hajek, A. E. (2004). *Natural Enemies: An Introduction to Biological Control*. Cambridge University Press, Cambridge.

Hatcher, M. J., Dick, J. T. A. & Dunn, A. M. (2006). How parasites affect interactions between competitors and predators. *Ecology Letters* **9**, 1253–1271.

Hattenschwiler, S. & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 1519–1524.

Hay, S. I., Packer, M. J. & Rogers, D. J. (1997). The impact of remote sensing on the study and control of invertebrate intermediate hosts and vectors for disease. *International Journal of Remote Sensing* **18**, 2899–2930.

Hay, M. E. & Taylor, P. R. (1985). Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* **65**, 591–598.

Hendrix, P. F. & Bohlen, P. J. (2002). Exotic earthworm invasions in North America: ecological and policy implications. *Bioscience* **52**, 801–811.

Hill, W., Ryon, M. & Schilling, E. (1995). Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* **76**, 1297–1309.

Hitchmough, J. & Wagner, M. (2011). Slug grazing effects on seedling and adult life stages of North American Prairie plants used in designed urban landscapes. *Urban Ecosystems* **14**, 279–302.

Ho, C.-K. & Pennings, S. C. (2008). Consequences of omnivory for trophic interactions on a salt-marsh shrub. *Ecology* **89**, 1714–1722.

Hogg, I. D. & Williams, D. D. (1996). Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* **77**, 395–407.

Holmes, G., Ortiz, J. C. & Schonberg, C. H. L. (2009). Bioerosion rates of the sponge *Cliona orientalis* Thiele, 1900: spatial variation over short distances. *Facies* **55**, 203–211.

Hooper, D., Chapin, F., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A., Vandermeer, J. & Wardle, D. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

Hughes, L. & Bazzaz, F. A. (2001). Effects of elevated co2 on five plant-aphid interactions. *Entomologia Experimentalis et Applicata* **99**, 87–96.

Huntly, P. M., Van Noort, S. & Hamer, M. (2005). Giving increased value to invertebrates through ecotourism. *South African Journal of Wildlife Research* **35**, 53–62.

Hutchings, P. A. (1986). Biological destruction of coral reefs: a review. *Coral Reefs* **4**, 239–252.

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. & Landis, D. (2009). Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* **7**, 196–203.

Jackson, J. K. & Fisher, S. G. (1986). Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* **67**, 629–638.

Jobbagy, E. & Jackson, R. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**, 423–436.

Jones, C. G., Lawton, J. H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* **69**, 373–386.

Jouquet, P., Dauber, J., Lagerlof, J., Lavelle, P. & Lepage, M. (2006). Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* **32**, 153–164.

Kellert, S. R. (1993). Values and perceptions of invertebrates. *Conservation Biology* **7**, 845–855.

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* **274**, 303–313.

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vazquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., et al. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* **10**, 299–314.

Kristensen, E. (1988). Benthic fauna and biogeochemical processes in marine sediments: microbial activities and processes. In *Nitrogen Cycling in Coastal Marine Environments* (eds T. A. Blackburn and J. Sorensen), pp. 275–279. John Wiley & Sons Ltd, Chichester.

Kristensen, E. & Alongi, D. M. (2006). Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. *Limnology and Oceanography* **51**, 1557–1571.

Kristensen, E. & Blackburn, T. H. (1987). The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. *Journal of Marine Research* **45**, 231–257.

Laakso, J. & Setala, H. (1999). Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* **87**, 57–64.

Lacey, L. A. & Orr, B. K. (1994). The role of bioloical-control of mosquitos in integrated vector control. *The American Journal of Tropical Medicine and Hygiene* **50**, 97–115.

Ladanyi, M. & Horvath, L. (2010). A review of the potential climate change impact on insect populations – General and agricutlural aspects. *Applied Ecology and Environmental Research* **8**, 143–152.

Lafferty, K. D., Dobson, A. P. & Kuris, A. M. (2006a). Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 11211–11216.

Lafferty, K. D., Hechinger, R. F., Shaw, J. C., Whitney, K. & Kuris, A. M. (2006b). Food webs and parasites in a salt marsh ecosystem. In *Disease Ecology: Community Structure and Pathogen Dynamics* (eds S. Collinge and C. Ray), pp. 119–134. Oxford University Press, New York.

Landis, D. A., Gardiner, M. M., van der Werf, W. & Swinton, S. M. (2008). Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 20552–20557.

Lavelle, P., Decaens, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. & Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology* **42**, S3–S15.

Lenat, D. R. (1988). Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of the North American Benthological Society* **7**, 222–233.

Lengyel, S., Gove, A. D., Latimer, A. M., Majer, J. D. & Dunn, R. R. (2009). Ants sow the seeds of global diversification in flowering plants. *PLoS ONE* **4**, e5480.

Leriche, H., LeRoux, X., Gignoux, J., Tuzet, A., Fritz, H., Abbadie, L. & Loreau, M. (2001). Which functional processes control the short-term effect of grazing on net primary production in grasslands? *Oecologia* **129**, 114–124.

Levenbach, S. (2008). Community-wide ramifications of an associational refuge on shallow rocky reefs. *Ecology* **89**, 2819–2828.

Losey, J. E. & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience* **56**, 311–323.

Luckenbach, M. W. & Orth, R. J. (1999). Effects of a deposit-feeding invertebrate on the entrapment of Zostera marina L. seeds. *Aquatic Botany* **62**, 235–247.

Luckhurst, B. E. & Luckhurst, K. (1978). Analysis of influence of substrate variables on coral-reef fish communities. *Marine Biology* **49**, 317–323.

Lundberg, J. & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* **6**, 87–98.

MacMahon, J. A., Mull, J. F. & Crist, T. O. (2000). Harvester Ants (*Pogonomyrex spp.*): their community and ecosystem influences. *Annual Review of Ecology and Systematics* **31**, 277–304.

Magni, P. & Montani, S. (2006). Seasonal patterns of pore-water nutrients, benthic chlorophyll a and sedimentary AVS in a macrobenthos-rich tidal flat. *Hydrobiologia* **571**, 297–311.

Mann, K. H. (1988). Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnology and Oceanography* **33**, 910–930.

Marcogliese, D. J. & Cone, D. K. (1997). Food webs: a plea for parasites. *Trends in Ecology & Evolution* **12**, 320–325.

Marcus, N. H. & Schmidt-Gengenbach, J. (1986). Recruitment of individuals into the plankton: the importance of bioturbation. *Limnology and Oceanography* **31**, 206–210.

McNickle, G. G., Rennie, M. D. & Sprules, W. G. (2006). Changes in benthic invertebrate communities of South Bay, Lake Huron following invasion by zebra mussels (Dreissena polymorpha), and potential effects on lake whitefish (Coregonus clupeaformis) diet and growth. *Journal of Great Lakes Research* **32**, 180–193.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J. & Schloss, A. L. (1993). Global climate change and terrestrial net primary production. *Nature* **363**, 234–240.

Melillo, J. N., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Magill, A., Ahrens, T. & Morrisseau, M. V. (2002). Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**, 2173–2176.

Memmott, J., Craze, P. G., Waser, N. M. & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* **10**, 710–717.

Menendez, R., Megias, A. G., Hill, J. K., Braschler, B., Willis, S. G., Collingham, Y., Fox, R., Roy, D. B. & Thomas, C. D. (2006). Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1465–1470.

Menge, B. A. (2000). Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* **250**, 257–289.

Metzger, R., Sartoris, F. J., Langenbuch, M. & Portner, H. O. (2007). Influence of elevated CO2 concentrations on thermal tolerance of the edible crab Cancer pagurus. *Journal of Thermal Biology* **21**, 144–151.

Meyers, N. (1997). Biodiversity's genetic library. In *Nature's Services: Societal Dependence on Natural Systems* (ed G. C. Daily), pp. 255–273. Island Press, Washington.

Meysman, F. J. R., Middelburg, J. J. & Heip, C. H. R. (2006). Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution* **21**, 688–695.

Moberg, F. & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics* **29**, 215–233.

Mooney, H. A. (2010). The ecosystem-service chain and the biological diversity crisis. *Philosophical Transactions of the Royal Society: Biological Sciences* **365**, 31–39.

Moore, J. W. (2006). Animal ecosystem engineers in streams. *Bioscience* **56**, 237–246.

Moraal, L. G. & Jagers op Akkerhuis, G. A. J. M. (2011). Changing patterns in insect pests on trees in The Netherlands since 1946 in relation to human induced habitat changes and climate factors-An analysis of historical data. *Forest Ecology and Management* **261**, 50–61.

Morin, A., Bourassa, N. & Cattaneo, A. (2001). Use of size spectra and empirical models to evaluate trophic relationships in streams. *Limnology and Oceanography* **46**, 935–940.

Mouritsen, K. N. & Poulin, R. (2002). Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* **124**, 101–117.

Mouritsen, K. N., Tompkins, D. M. & Poulin, R. (2005). Climate warming may cause a parasite-induced collapse in coastal amphipod populations. *Oecologia* **146**, 476–483.

Murray, J. M. H., Meadows, A. & Meadows, P. S. (2002). Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. *Geomorphology* **47**, 15–30.

Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology* **12**, 39–45.

Naeem, S., Buner, D. E., Hector, A., Loreau, M. & Perrings, C. (2009). *Biodiversity, Ecosystem Funtioning, and Human Wellbeing*. Oxford Press, New York.

Nakano, S. & Murakami, M. (2001). Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 166–170.

Neumann, A. C. (1966). Observations on coastal erosion in Bermuda and measurements of boring rate of sponge *Cliona Lampa*. *Limnology and Oceanography* **11**, 92–108.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. & Favila, M. E. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* **141**, 1461–1474.

Ohkawara, K., Higashi, S. & Ohara, M. (1996). Effects of ants, ground beetles and the seed-fall patterns on myrmecochory of *Erythronium japonicum* Decne (Liliaceae). *Oecologia* **106**, 500–506.

Paine, R. T. (1969). The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology* **50**, 951–961.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637–669.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Pennings, S. C., Ho, C.-K., Salgado, C. S., Więski, K., Dave, N., Kunza, A. E. & Wason, E. L. (2009). Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology* **90**, 183–195.

Pinn, E. H., Thompson, R. C. & Hawkins, S. J. (2008). Piddocks (Mollusca : Bivalvia : Pholadidae) increase topographical complexity and species diversity in the intertidal. *Marine Ecology-Progress Series* **355**, 173–182.

Pointier, J. P. & Jourdane, J. (2000). Biological control of the snail hosts of schistosomiasis in areas of low transmission: the example of the Caribbean area. *Acta Tropica* **77**, 53–60.

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of Intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**, 297–330.

Polis, G. A. & Strong, D. R. (1996). Food web complexity and community dynamics. *American Naturalist* **147**, 813–846.

Pomeroy, L. R., D'Elia, C. F. & Schaffner, L. C. (2006). Limits to top-down control of phytoplankton by oysters in Chesapeake Bay. *Marine Ecology Progress Series* **325**, 301–309.

Pongsiri, M. J., Roman, J., Ezenwa, V. O., Goldberg, T. L., Koren, H. S., Newbold, S. C., Ostfeld, R. S., Pattanayak, S. K. & Salkeld, D. J. (2009). Biodiversity loss affects global disease ecology. *Bioscience* **59**, 945–954.

Post/AP, Huffington. (2009). Jumbo squid invasion: "Carnivorous Calamari" invade San Diego shores, spook divers. *Huffington Post*, vol. 17 July, 2009, San Diego.

Poulin, R. & Morand, S. (2000). The diversity of parasites. *The Quarterly Review of Biology* **75**, 277–293.

Primack, R. (1993). *Essentials of Conservation Biology*. Sinauer Associates, Sunderland.

Rafferty, N. E. & Ives, A. R. (2011). Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology Letters* **14**, 69–74.

Reaka-Kudla, M. L., Feingold, J. S. & Glynn, W. (1996). Experimental studies of rapid bioerosion of coral reefs in the Galapagos Islands. *Coral Reefs* **15**, 101–107.

Regnier, E., Harrison, S. K., Liu, J., Schmoll, J. T., Edwards, C. A., Arancon, N. & Holloman, C. (2008). Impact of an exotic earthworm on seed dispersal of an indigenous US weed. *Journal of Applied Ecology* **45**, 1621–1629.

Reichardt, W. (1988). Impact of bioturbation by *Arenicola marina* on microbiological parameters in intertidal sediments. *Marine Ecology Progress Series* **44**, 149–158.

Rey, J. R., O'Connell, S., Suarez, S., Menendez, Z., Lounibos, L. P. & Byer, G. (2004). Laboratory and field studies of Macrocyclops albidus (Crustacea : Copepoda) for biological control of mosquitoes in artificial containers in a subtropical environment. *Journal of Vector Ecology* **29**, 124–134.

Rhoads, D. C. & Young, D. K. (1970). Influence of feposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28**, 150–178.

Richards, P. J. (2009). *Aphaenogaster* ants as bioturbators: impacts on soil and slope processes. *Earth-Science Reviews* **96**, 92–106.

Rojas, M. R., Locatelli, B. & Billings, R. (2010). Climate change and outbreaks of Southern pine beetle Dendroctonus frontalis in Honduras. *Forest Systems* **19**, 70–76.

Roth, S. K. & Lindroth, R. L. (1994). Effects of co2-mediated changes in paper birch and white-pine chemistry on gypsy-moth performance. *Oecologia* **98**.

Sachs, J. & Malaney, P. (2002). The economic and social burden of malaria. *Nature* **415**, 680–685.

Sagarin, R. D., Barry, J. P., Gilman, S. E. & Baxter, C. H. (1999). Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* **69**, 465–490.

Samish, M. & Rehacek, J. (1999). Pathogens and predators of ticks and their potential in biological control. *Annual Review of Entomology* **44**, 159–182.

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* **40**, 245–269.

Schmitz, O. J., Hamback, P. A. & Beckerman, A. P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* **155**, 141–153.

Schowalter, T. D. (2011). *Insect Ecology: An Ecosystem Approach*. Third Edition. Academic Press, Boston.

Seastedt, T. R. (1984). The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* **29**, 25–46.

Shafroth, P. B., Cleverly, J. R., Dudley, T. L., Taylor, J. P., Van Riper, C., Weeks, E. P. & Stuart, J. N. (2005). Control of Tamarix in the western United States: implications for water salvage, wildlife use, and riparian restoration. *Environmental Management* **35**, 231–246.

Silliman, B. R. & Bertness, M. D. (2002). A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences* **99**, 10500–10505.

Simberloff, D. & Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* **1**, 21–32.

Simon, K. S., Simon, M. A. & Benfield, E. F. (2009). Variation in ecosystem function in appalachian streams along an acidity gradient. *Ecological Applications* **19**, 1147–1160.

Snaddon, J. L., Turner, E. C. & Foster, W. A. (2008). Children's perceptions of rainforest biodiversity: which animals have the lion's share of environmental awareness. *PLoS ONE* **3**, e2579.

Southward, J. L., Hawkins, S. J. & Burrows, M. T. (1995). Seventy years of observations of changes in distribution and abundance of zooplankton and intertidal organisms in the Western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* **20**.

Southwick, E. E. & Southwick, L. (1992). Estimating the economic value of honey bees (Hymenoptera, Apidae) as agricultural pollinators in the United-States. *Journal of Economic Entomology* **85**, 621–633.

Spooner, D. E. & Vaughn, C. C. (2006). Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology* **51**, 1016–1024.

Spooner, D. E. & Vaughn, C. C. (2008). A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. *Oecologia* **158**, 307–317.

Spurgeon, J. P. G. (1992). The economic valuation of coral reefs. *Marine Pollution Bulletin* **24**, 529–536.

Srivastava, D. S., Cardinale, B. J., Downing, A. L., Duffy, J. E., Jouseau, C., Mahesh, S. & Wright, J. P. (2009). Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* **90**, 1073–1083.

Stachowicz, J. J., Bruno, J. F. & Duffy, J. E. (2007). Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **38**, 739–766.

Stadler, B., Muller, T. & Orwig, D. (2006). The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. *Ecology* **87**, 1792–1804.

Statzner, B., Bonada, N. & Doledec, S. (2007). Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate communities: a case for a collective public database. *Biodiversity and Conservation* **16**, 3609–3632.

Strayer, D. L., Caraco, N. F., Cole, J. J., Findlay, S. & Pace, M. L. (1999). Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. *Bioscience* **49**, 19–27.

Stromberg, J. C., Lite, S. J., Marler, R., Paradzick, C., Shafroth, P. B., Shorrock, D., White, J. M. & White, M. S. (2007). Altered stream-flow regimes and invasive plant species: the Tamarix case. *Global Ecology and Biogeography* **16**, 381–393.

Swan, C. M. & Palmer, M. A. (2006). Preferential feeding by an aquatic consumer mediates non-additive decomposition of speciose leaf litter. *Oecologia* **149**, 107–114.

Swank, W. T., Waide, J. B., Crossley, D. A. & Todd, R. L. (1981). Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia* **51**, 297–299.

Swift, M., Heal, O. & Anderson, J. (1979). *Decomposition in Terrestrial Ecosystems*. University of California Press, Berkeley.

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. & Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577–581.

Thompson, L., Thomas, C. D., Radley, J. M. A., Williamson, S. & Lawton, J. H. (1993). The effect of earthworms and snails in a simple plant community. *Oecologia* **95**, 171–178.

Traill, L. W., Lim, M. L. M., Sodhi, N. S. & Bradshaw, C. J. A. (2010). Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology* **79**, 937–947.

Tuchman, N. C., Wetzel, R. G., Rier, S. T., Wahtera, K. A. & Teeri, J. A. (2002). Elevated atmospheric co2 lowers leaf litter nutritional quality for stream ecosystem food webs. *Global Change Biology* **8**, 163–170.

Turke, M. E., Heinze, E., Andreas, K., Svendsen, S. M., Gossner, M. M. & Weisser, W. W. (2010). Seed consumption and dispersal of ant-dispersed plants by slugs. *Oecologia* **163**, 681–693.

Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Global Change Biology* **11**, 1351–1363.

Underwood, E. C. & Fisher, B. L. (2006). The role of ants in conservation monitoring: if, when, and how. *Biological Conservation* **132**, 166–182.

U.S. Department of the Interior, Fish and Wildlife Service, U.S. Department of Commerce & Bureau, U.S.C (2006). National survey of fishing, hunting and wildlife-associated recreation.

Van der Putten, W. H., Macel, M. & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2025–2034.

Vanninen, I., Worner, S., Huusela-Veistola, E., Tuovinen, T., Nissinen, A. & Saikkonen, K. (2011). Recorded and potential alien invertebrate pests in Finnish agriculture and horticulture. *Agricultural and Food Science* **20**, 96–113.

Volkenborn, N., Hedtkamp, S. I. C., van Beusekom, J. E. E. & Reise, K. (2007). Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuarine, Coastal and Shelf Science* **74**, 331–343.

Volney, W. J. A. & Fleming, R. A. (2000). Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment* **82**, 283–294.

Vorosmarty, C. J. & Sahagian, D. (2000). Anthropogenic disturbance of the terrestrial water cycle. *Bioscience* **50**, 753–765.

Wall, D. H. (2007). Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**, 2291–2306.

Wall, D. H. & Moore, J. C. (1999). Interactions underground- Soil biodiversity, mutualism, and ecosystem processes. *Bioscience* **49**, 109–117.

Wallace, J. B. & Webster, J. R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, 115–139.

Wallin, K. F. & Raffa, K. F. (2001). Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? *Ecology* **82**, 1387–1400.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature* **416**, 389–395.

Wardle, D. A. (2002). *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton.

Weisser, W. & Siemann, E. (2004). The various effects of insects on ecosystem functioning. In *Insects and Ecosystem Function. Ecological Studies* (eds W. Weisser and E. Siemann), pp. 3–24. Springer-Verlag, Berlin, Heidelberg.

Werner, E. & Peacor, S. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083–1100.

Widdicombe, S., Austen, M. C., Kendall, M. A., Warwick, R. M. & Jones, M. B. (2000). Bioturbation as a mechanism for setting and maintaining levels of diversity in subtidal macrobenthic communities. *Hydrobiologia* **440**, 369–377.

Wilkinson, C. R. (1996). Global change and coral reefs: impacts on reefs, economies and human cultures. *Global Change Biology* **2**, 547–558.

Willems, J. H. & Huijsmans, K. G. A. (1994). Vertical seed dispersal by earthworms: a quantitative approach. *Ecography* **17**, 124–130.

Wilson, E. O. (1987). The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* **1**, 344–346.

Wilson, R. J., Gutierrez, D., Gutierrez, J. & Monserrat, V. J. (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* **13**, 1873–1887.

Wise, D., Snyder, W., Tuntibunpakul, P. & Halaj, J. (1999). Spiders in decomposition food webs of agroecosystems: theory and evidence. *Journal of Arachnology* **27**, 363–370.

Worm, B. & Duffy, J. E. (2003). Biodiversity, productivity and stability in real food webs. *Trends in Ecology & Evolution* **18**, 628–632.

WRI (World Resources Institute). (2003). *Millenium Ecosystem Assessment, Ecosystems and Human Wellbeing: A Framework for Assessment*. Island Press, Washington.

Yang, L. H. (2004). Periodical cicadas as resource pulses in North American forests. *Science* **306**, 1565–1567.

Yang, L. H., Bastow, J. L., Spence, K. O. & Wright, A. N. (2008). What can we learn from resource pulses? *Ecology* **89**, 621–634.

Yusa, Y. (2006). Predators of the introduced apple snail, Pomacea canalicultata (Gastropoda: Ampullariidae): their effectiveness and utilisation in biological control. In *Global Advances in Ecology and Management of Golden Apple Snails* (eds R. C. Joshi and L. S. Sebastian, pp. 345–361). Philippine Rice Research Institute, Munoz.

Zvereva, E. L. & Kozlov, M. V. (2006). Consequences of simultaneous elevation of carbon dioxide and temperature for plant herbivore interactions: a metaanalysis. *Global Change Biology* **12**, 26–34.

IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. References used in search discussed in Section II.

Appendix S2. References used in Table 3.

Table S1. Number of relevant papers across different journals. The relevant papers are widespread across journals, except for many papers (14) in Global Change Biology (table 3).

(*Received 15 January 2012; revised 20 October 2012; accepted 1 November 2012; published online 6 December 2012*)