Title: Effects of Sea Ice on Arctic biota: an emerging crisis discipline

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## Abstract

The rapid decline in Arctic sea ice *(ASI)* extent, area and volume during recent decades is occurring before we can understand many of the mechanisms through which *ASI* interacts with biological processes both at sea and on land. As a consequence, our ability to predict and manage the effects of this enormous environmental change is limited, making this a *crisis discipline*. Here, we propose a framework to study these effects, defining *direct effects* as those acting on life history events of Arctic biota, and *indirect effects*, where *ASI* acts upon biological systems through chains of events, normally involving other components of the physical system and/or biotic interactions. Given the breadth and complexity of *ASI*'s effects on Arctic biota, Arctic research requires a truly multidisciplinary approach to address this issue. In the absence of effective global efforts to tackle anthropogenic global warming, *ASI* will likely continue to decrease, compromising the conservation of many *ASI*-related taxonomic groups and ecosystems. Mitigation actions will heavily rely on the knowledge acquired on the mechanisms and components involved with the biological effects of *ASI*.

## Keywords

Sea ice, Arctic Biota, Arctic Ecology, Climate Change, Conservation, Crisis Discipline

## Main text

### 1. Introduction

The extent, area, and volume of Arctic Sea Ice *(ASI)* have shrunk sharply in the past decades: these changes are occurring most especially, but not exclusively, in minimum late summer extent [1, 2], and a seasonally ice-free Arctic Ocean is predicted by the mid-21st century [3]. High temperatures (*radiative/thermal forcing*) and atmospheric circulation controlling sea ice export out of the Arctic Ocean (*dynamic/wind forcing*) have been identified as *ASI* drivers [4-7]. *ASI* is also a key driver of Arctic climate, feeding back on regional and global climate and modifying both water and energy budgets. Its high albedo and low thermal conductivity are key to *i)* reflect a large part of the incoming solar radiation (*albedo feedback*); *ii)* prevent heat transfers from the relatively warm ocean to the cold atmosphere in autumn and winter (*conduction feedback*); and *iii)* prevent the atmospheric boundary layer from picking up moisture (*cloud-ice feedback*). Further, *iv) ASI* influences the formation of deep water in the North Atlantic [8]. Together with feedbacks linked to the presence of snow and ice on land, these processes constitute an important component of the large temperature oscillations recorded in the Arctic (i.e. faster rates of climate change than at lower latitudes), known as Arctic Amplification [AA; 9], which has been operating since the Cretaceous [10]. Non-*ASI*-related processes also play important roles in the *AA*, such as temperature feedbacks in the vertical structure of the warming (*lapse-rate feedback*) and the relationship between radiative forcing, temperature, and longwave emission (*Planck's feedback*) [9, 11]. The net effect of *ASI* dynamics on climate (in the Arctic and beyond) is yet unquantified, constituting a highly active research area. Its proposed impacts range from positive regional warming, changes in hemispheric atmospheric circulation patterns, sea surface temperature dynamics, the marine carbon cycle, ocean acidification, to abrupt cooling events (Electronic Supplementary Material 1, hereafter ESM1).

## 2. Ecological Impacts of *ASI*

*ASI* dynamics are known to impact Arctic biota (marine and terrestrial) adapted to – or at least affected by – its presence. *ASI* may affect life history events of arctic biota directly (*direct effects*), or through chains of events (*indirect effects*) involving the modification of components of the physical system (mostly weather/climate and geomorphological processes such as coastal erosion) and/or biotic interactions, or through a combination of both (*compound effects*) (Figure 1).

### *2.1. Direct effects*

Many organisms interact with sea ice cover, which can serve as a *i)* living medium, *ii)* transport/mobility-affecting structure, or *iii)* resource filter (Figure 1).

**Living medium**. Multiple taxonomic groups inhabit the diversity of habitats provided by the *ASI* matrix. This include *a)* nutrient-poor *melt ponds*, which can become highly productive if the underlying sea ice melts completely; *b)* inhospitable and hypersaline *interior layers* of solid ice, where microbial communities flourish within the brine draining system; *c)* highly productive *bottom- and platelet-ice*, rich in algal and microbial biomass; and *d)* suspended and large diatom communities attached to the bottom of sea ice (*strand communities*) [12]. *ASI* reduction translates into changes in abundance, distribution, composition, and seasonality of these highly adapted communities. Many other animals actively or passively use *ASI* as a structure to hunt, mate, rest, whelp, rear offspring, or avoid predators. Moore and Huntington [13] evaluated the *ASI*-dependence of Arctic mammal species, recognising ***1)*** *ice-obligate species* – requiring ice as a platform for resting, breeding, and/or hunting, such as polar bear (*Ursus maritimus* Phipps, 1774), walrus (*Odobenus rosmarus* (Linnaeus, 1758)), or bearded (*Erignathus barbatus* (Erxleben, 1777)) and ringed (*Pusa hispida* (Schreber, 1775)) seals; ***2)*** *ice-associated species* – those adapted to the Arctic marine ecosystem, using *ASI* for whelping or feeding, such as harp (*Pagophilus groenlandicus* (Erxleben, 1777)), hooded (*Cystophora cristata* (Erxleben, 1777)), ribbon (*Histriophoca fasciata* (Zimmerman, 1783)), and spotted (*Phoca largha* (Pallas, 1811)) seals, or bowhead (*Balaena mysticetus* Linnaeus, 1758), beluga (*Delphinapterus leucas* (Pallas, 1776)), and narwhal (*Monodon monoceros* Linnaeus, 1758) whales; and ***3)*** *seasonally migrant species*, such as fin (*Balaenoptera physalus* (Linnaeus, 1758)), minke (*Balaenoptera acutorostrata* Lacépède, 1804), humpback (*Megaptera novaeangliae* (Borowski, 1781)), grey (*Eschrichtius robustus* (Lilljeborg, 1861)) and killer (*Orcinus orca* (Linnaeus, 1758)) whales. This classification can be applied to other taxa: the spectacled eider (*Somateria fischeri* (Brandt, 1847)) uses pack ice as a wintering ground [14] and is thus an *ice-obligate* species. The arctic cod (*Boreogadus saida* (Lepechin, 1774)), which is a primary prey of narwhal, beluga, ringed seal, and seabirds, is well adapted to *ASI* (finding protection from predation under rugged sea ice), but also found in ice-free areas, being thus an *ice-associated species*. *Ice-obligate species* are predicted to undergo decreased fitness with declining *ASI*; *ice-associated species* to show trade-offs between opportunities and increased competition; and *seasonally migrant species* to benefit from it [13].

**Transport/mobility structure**. *ASI* has been reported to directly affect the migration and/or seasonal movement patterns of multiple taxa [15, ESM1]. In general, *ASI* has been seen as a barrier to movement for many marine species, effectively isolating populations [e.g. walrus; 16]. At a smaller scale, Laidre *et al.* [17; this feature] found that reduced sea ice extent and seasonal duration makes the fjords of large and wide tidewater glaciers in Greenland, abundant in clear freshwater, increasingly accessible to narwhals (which, like belugas, they are attracted to). *ASI* has also been proposed as an effective long-distance dispersal platform for many terrestrial plants, lichens, fungi, and animals, including benthic intertidal species (ESM1). As early as 1925, Bristowe [18] proposed sea ice bridges connecting Jan Mayen and Greenland as transport platforms for Arctic foxes (*Vulpes lagopus* L.). Indeed, genetic evidence points to *ASI* being very important for the connectivity between populations of Arctic foxes [19, pan-Arctic], and wolf (*Canis lupus* L.) and caribou (*Rangifer tarandus* L.) in the Canadian Arctic Archipelago [CAA; 20, ESM1]. Jenkins *et al.* [21; this feature] used genetic fingerprinting and geodesic distance between populations to infer that sea ice had acted as an effective connectivity landscape feature for Peary caribou in the *CAA*. They estimated that landscape resistance has increased by approximately 15% since 1979 due to sea ice loss. Bristowe [18] further pointed to sea ice-encased driftwood as the means for insects and plants to reach Jan Mayen. Seeds of many circum-Arctic plants and propagules of lichens may not only drift with *ASI*, but also travel long distances over it pushed by wind [22, ESM1], being deposited on ice and re-entrained by wind in ways not facilitated by an open-water ocean. This has long been proposed as a key mechanism in the amphi-Atlantic and West-Arctic elements of Arctic flora described by Hultén [23, 24]. Supporting it, Alsos *et al.* [25; this feature] provide evidence for first colonisation dates of 102 vascular plant species in Svalbard related to abundant sea ice as inferred from palaeo-environmental data.

**Resource filter**. *ASI* can act as a very effective resource filter, such as in regulating the amount of light that reaches the upper layers of the ocean, which in turn affects ocean productivity and carbon sequestration [12, ESM1]. Kahru *et al.* [26; this feature] report a ~47% increase in pan-Arctic monthly maximum phytoplankton primary productivity, and an advance of up to 50 days in the annual timing of phytoplankton blooms in the Arctic Ocean (from 1997-2015), as a result of increased open water extent and duration of the open water season.

### *2.2. Indirect effects*

Indirect effects of *ASI* on Arctic biota are numerous and widespread, some even reaching lower latitudes [e.g. 27]. They can be broadly classified as *i)* modification of the physical system and *ii)* biological interactions (Figure 1).

**Modification of the physical system.**

*Climate/weather modification. ASI*'s modification of local and/or regional weather and climate may affect many ecological systems. Most indirect effects on terrestrial tundra are linked to *ASI*/*AA* feedbacks. For example, increased tundra primary productivity has been linked to such feedbacks, with higher ambient temperatures favouring increased productivity of some tundra plants, especially deciduous shrubs [28, ESM1], as have fungal community composition shifts [29; this feature]. Other proposed indirect effects include moisture limitation linked to declining *ASI* and thus reduced plant productivity [30; this feature]. Post *et al.* [31; this feature] report on individualistic rates of phenological change in tundra plants of Western Greenland over a 12yr period, with early-emerging species displaying stronger relationships with *ASI*, advancing their emergence more than late-emerging ones: here, *ASI* is assumed to modify a suite of local climate conditions key to local plant phenology. Recently, arctic terrestrial vegetation has also been shown to be locally controlled by sea ice influence on weather in Svalbard [32].

*Modification of Geomorphological Processes*. *ASI* controls coastal erosion rates by governing fetch and wave action. *ASI*-induced increased erosion rates can lead to major changes in coastal environments, as well as affecting sediment supply to adjacent continental shelf waters and their ecosystems by affecting e.g. primary productivity [33, ESM1]. Chains of indirect effects involving weather/climate and geomorphological processes are possible (e.g. *ASI*-modified weather impacting the active layer and eventually terrestrial and freshwater ecosystems).

**Biological interactions**. Direct/indirect effects of *ASI* on biotic components may modify others (e.g. through trophic relations, such as West Greenland's *phenological community* shifts enhancing *trophic mismatch* between plants and caribou [34]). The assemblages of archaea, bacteria, microalgae, protists, and metazoans (cnidarians, rotifers, nematodes, nudibranchs, larvae of molluscs, annelids, amphipods, copepods, euphausiids, and small fish) living within the *ASI* matrix are preyed by a host of pelagic animals and, when dead, descend through the water column providing food to benthic ecosystems [12].

Many seabirds are associated with *bottom-up* processes driven by *ASI*, as shown in sea ice spring retreat times driving phytoplankton and thus zooplankton abundances. These drive population numbers of walleye pollock (*Gadus chalcogrammus* Pallas, 1814) on which seabirds rely in the Bering Sea [35; this feature]. Mandt's black guillemot's (*Cepphus grylle mandtii* (Lichtenstein, 1822)) and ivory gull's (*Pagophila eburnean* (Phipps, 1774)) show a year-round association with the marginal sea ice zone and high sea ice concentrations for roosting (direct effect; Mandt's black guillemots) and prey availability (indirect, both) [36, 37; this feature]. Increased phytoplankton productivity [26; this feature] indirectly affects organisms that feed on photosynthetic microorganisms and thus depend on its altered distribution and timing, observed in the recent northward shift in the Bering Sea ecological assemblages, or in the dependence of some Arctic marine mammals on *ASI*-dwelling prey (ESM1). Increased availability of *in situ* produced copepods and euphausiids advected from the south through the Bering Strait boosts food delivery to baleen whales in the Pacific Arctic region, and although new seasonally ice-free areas enhance the influx of subarctic species (e.g. humpback, fin and minke whales), which may result in resource competition with Arctic bowhead and grey whales, this might be limited by both migration timing and species-specific foraging capabilities – *habitat partitioning* [38; this feature].

However, the effects of sub-Arctic seasonal migrants are not always neutral, even in the presence of ample prey abundance. O'Corry-Crowe *et al*. [39; this feature] show that despite their highly adaptive behaviour to changing *ASI* conditions and strong philopatry, beluga whales modified their spring migration routes in highly anomalous sea ice years in response to increased occurrence of predatory killer whales. This finding is in line with a progressive *borealisation* of fish communities in the Arctic linked to *ASI* decline [40]. Interestingly, some of these responses differed between sexes, highlighting sex-asymmetrical adaptations to *ASI*. Further, changes in the distribution of Arctic species and the expansion of sub-Arctic species in response to *ASI* decline will cause new interactions, potentially including local competitive exclusion of adapted Arctic species and/or effects through the trophic chain. *ASI*'s decline might show very different indirect effects on Arctic dwellers depending on their prey. For instance, walrus and bearded seals prey on benthic bivalves supported by a tight pelagic–benthic coupling transferring ice-associated production to the sea floor, and might thus suffer from its decoupling if *ASI* recedes to deeper ocean areas. In contrast, reduced sea ice is hypothesized to favour pelagic over benthic production [13, ESM1] and thus increase food availability to piscivorous ringed seals (but note that ringed seals also require *ASI* as a platform to rest and breed – see section 2.1).

Biological Interactions include human activities, which span from traditional subsistence activities to industrial fishing, natural resource extraction, and international sea transport, the latter three adding further pressure to *ASI*-dependent Arctic biota (e.g. disrupted caribou migration by human-induced sea ice breaking; ESM1) and being Arctic sources of greenhouse gas emissions. Mass reindeer starvation and its consequences for Nenets herders was linked to winter sea ice loss in the Barents and Kara Seas [41; this feature]. Open ocean water promoted moisture delivery and unseasonably above-freezing temperatures on the adjacent Yamal Peninsula, resulting in extensive rain-on-snow and the formation of an ice crust on the snow once normal temperatures returned that prevented reindeer from feeding. Technological advances can help practitioners of subsistence activities adapting to the changing environment: powerful and fuel-efficient out-board engines aid subsistence hunters in Northern Alaska in adapting to *ASI*-modified migration times, distribution and behaviour of marine mammals [42; this feature]. However, this is jeopardised by the increased industrial activity linked to fossil fuel extraction and transportation.

#### *2.2.1. <u>Compound effects</u>*

Whereas conceptualising the effects of *ASI* on Arctic biota as direct or indirect is useful for determining the nature of these interactions, compound effects (where direct and indirect effects act in combination) are expected to be the norm at the ecosystem level. These can be seen as complex indirect effects. Polar bears use *ASI* as a hunting platform and as a transportation platform [in turn affected by drift; 43; direct effect]. Indeed, the statistical relationship between polar bear numbers and *ASI* duration was the basis to forecast the species' decline [44; this feature]. However, the interactions between polar bears and *ASI* are more nuanced. Their main sources of prey, bearded and ringed seals, are *ASI*-associated year-round for rearing pups and moulting. Ringed seals require early *ASI* so that enough snow accumulates on to construct lairs, whereas bearded seals require *ASI* over shallow waters to prey on benthic communities [45]. *ASI*'s direct effects on these species cascade to polar bears: some polar bear individuals have been reported to increase predation on ground-nesting seabird colonies as a response to seal scarcity, further affecting other taxa [46; indirect effects]. Further, *ASI*'s direct effect on marine primary productivity drives all other trophic levels (including polar bears; indirect effects).

Thus, *ASI* affects polar bear populations directly, indirectly, and through the interaction of direct and indirect effects (biotic and abiotic).

## 3. A Crisis Discipline

Information on the interactions between *ASI* and Arctic biota is obtained from observations and proxy data. Observations consist largely of *1)* extremely valuable, spatially patchy and temporally short studies, *2)* a wealth of less quantitative and often undervalued traditional ecological knowledge (*TEK*), and *3)* increasingly rich and available remote sensing data. Cold Arctic environments generally favour the preservation of a range of proxy biological and environmental records, such as ancient DNA and organic matter preserved in the permafrost [e.g. 47]. However, low sedimentation rates in the Arctic Ocean, and the frequent glacial/periglacial disturbance in depositional environments on land (including ebbs and flows of valley glaciers and ice sheets, large oscillations in sea level resulting in marine transgressions and regressions in the lowlands, and active layer processes) limit and bias the quality and availability of sedimentary sequences.

Such data gaps (i.e. patchy, short observations, and challenging proxy material) limit our understanding of Arctic biota's association with and response to environmental change, and exist at a time of extreme *ASI* decline; the study of the dependence of Arctic biota to *ASI* thus qualifies as a *crisis discipline*, according to the criteria proposed by Soulé [48] in the context of *Conservation Biology*. In *crisis disciplines*, decisions need to be made (i.e. urgency exists) in the face of large uncertainty. Ceballos *et al.* [49] reported on alarming rates of species extinctions and abundance and range reductions, with high latitudes showing higher-to-much-higher than average reductions (relative to their overall richness) in birds and mammals. They enumerated 6 main global drivers of biodiversity loss that are applicable to *ASI's* consequences on ecological processes, namely:

**A. Habitat conversion** (fragmentation/land cover change): whereas *ASI* decline tends to enhance gene flow between populations of marine species and hence can be seen as a landscape de-fragmentation, it also decreases the connectivity between populations of many taxonomic groups that use *ASI* as a means of transport (actively or passively), increasing *landscape resistance*. Moreover, through changing the conditions in the photic zone of the ocean, *ASI*'s decline modifies primary productivity, with generalised bottom-up consequences across all trophic levels.

**B. Climate disruption/climate change**: current changes in *ASI* are a direct consequence of changes in climate, and *ASI* dynamics are linked to feedbacks with climate, in particular the *AA*, thereby accelerating climate change in the region (and potentially beyond) and adding further stress to Arctic biota.

**C. Species invasions**. The disappearance of *ASI* and the warming of Arctic Ocean waters facilitates the range expansion of sub-Arctic marine species into the Arctic [40]. However, less *ASI* has also been linked with reduced long-distance transport of terrestrial taxa, thus reducing the likelihood of invasions of many terrestrial species onto Arctic islands, although this might be offset by *i)* increased trade routes, mobility, and human presence, and *ii)* improved conditions for the successful establishment of many terrestrial taxa in the

Arctic, both in turn affected by *ASI*. The net effect of species invasions on Arctic biodiversity will depend on the degree to which, and pace at which, these can outcompete, displace, and eventually eliminate Arctic-adapted taxa.

**D. Toxification/pollution**. *ASI* decrease enhances the circulation of pollutants in the Arctic Ocean [50]. Moreover, increased marine traffic and human presence in the region increase *in situ* pollution. Further compounding this issue is evidence that *i)* global surface circulation currents accumulate plastics and other debris from more polluting and densely populated regions of Earth in the more accessible, low *ASI* Arctic Ocean [51], and *ii)* contaminants delivered to the Arctic Ocean by rivers (originated through human activities, but also from enhanced permafrost melt) are affected by the dynamics of *ASI* [e.g. 52].

**E. Overexploitation /overharvesting**. Many of *ASI*'s effects on Arctic biota, notably on mammals, occur against a background of historical overexploitation that reduced population numbers, genetic variability, and distribution ranges, likely establishing legacies on their ability to respond to present changes. For example, Alter *et al.* [53] show much lower present bowhead whales' genetic diversity when compared with historical populations, and current grey whale numbers (~22,000) are estimated to be ~3-5 times lower than pre-whaling [54].

**F. Disease**. Although largely unknown and unquantified, *ASI* decline may be linked with disease dynamics by rendering the Arctic *i)* more accessible to large-scale human activities, *ii)* warmer, and *iii)* more amenable to species invasions. Further, species affected by *ASI* decline might show an increased number of weakened/stressed individuals, rendering them more susceptible to disease. Indirectly, *ASI* decline contributes to enhanced *AA* and thus melting of the permafrost, which has already caused disease outbreaks, e.g. Anthrax outbreak in Yamal [55].

## 4. Conclusion

Accelerated climate change in the Arctic has brought the region beyond the 2°C safety threshold (e.g. https://data.giss.nasa.gov/gistemp/) recently agreed in Paris under the United Nations Framework Convention on Climate Change [UNFCCC; 56], *ASI*'s decline rates having made even the boldest model projections fall short [e.g. 57]. With daily anomalies exceeding +16°C in many high Arctic locations during the 2016/7 winter, and such events becoming more frequent [58], a 'new normal' cannot be safely defined, since the region's climate – and environment – are in the midst of a sharp transition.

Given the breadth and complexity of the effects that *ASI* exerts on Arctic biota (full-year or seasonally resident) and their interactions, Arctic research requires a truly multidisciplinary approach to address the biological consequences of such pressing environmental change (across all groups, from microorganisms and invertebrates to traditionally more studied taxa such as large marine mammals). Traditional site-based ecological studies (plus marine studies performed along the routes of oceanographic expeditions) need to be complemented with information not only derived from other disciplines such as remote sensing, climate/sea ice modelling, glaciology, geomorphology, oceanography, physiology, palaeo-ecology, palaeo-climatology, and molecular ecology, but also from the extensive TEK of Arctic peoples.

The present special feature covers a wide range of these disciplines and demonstrates that a large body of knowledge already exists on the relationship between *ASI* and Arctic biota. A systematic review [e.g. 59] would help identify where the existing evidence on the effects of *ASI* on arctic biota resides across all these disciplines, and where the most pressing gaps (geographical, taxonomical, technical, and/or conceptual) lie. *ASI*-related ecological consequences are difficult to mitigate directly, since only a global effort to address climate warming would potentially reverse current *ASI* trends [e.g. 2]. In the absence of effective global action, *ASI* will most likely continue to decline [3]. Only by understanding the mechanisms that link *ASI* to Arctic biota, will we be in the position to anticipate future scenarios, manage the present crisis, and target processes that have the potential to interact with *ASI* decline, such as anthropogenic pressure in the form of increased large-scale activities or pollution.

## Figure/table legends (where used)

**Figure 1: Arctic Sea Ice *(ASI)* effects on Arctic biota.** *Direct* (**continuous line**): *ASI* modifies Arctic biota's life history events, acting as a *(**A**)* living medium [44; this feature], *(**B**)* transport/mobility-affecting structure [17, 21, 25; this feature], or *(**C**)* resource filter [26; this feature]. *Indirect* (**discontinuous line**): *ASI* affects Arctic biota through chains of events, normally involving *(**D**)* physical system modification [29, 30, 31; this feature] and/or *(**E**)* biotic interactions [35-38, 39; this feature], which include *(**E1**)* human activities [41, 42; this feature], or through combinations of *Direct* and *Indirect Effects* (*Compound effects*, see text*). Bidirectional arrow* in ***D*** indicates feedbacks between *ASI* and *Other components of the physical system,* which can modulate *ASI*'s *Indirect Effects* on Arctic biota. *Arrow cycles* indicate possible interactions within *Other components of the physical system* (e.g. *ASI* affecting climate, which in turn affects geomorphology, which indirectly affects Arctic biota) or *Arctic biota* (e.g. *ASI*'s triggered trophic chain responses).

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## Author contributions

MM-F designed and wrote the manuscript. EP co-designed the study and contributed to the manuscript.

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We have no competing interests.

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N/A.

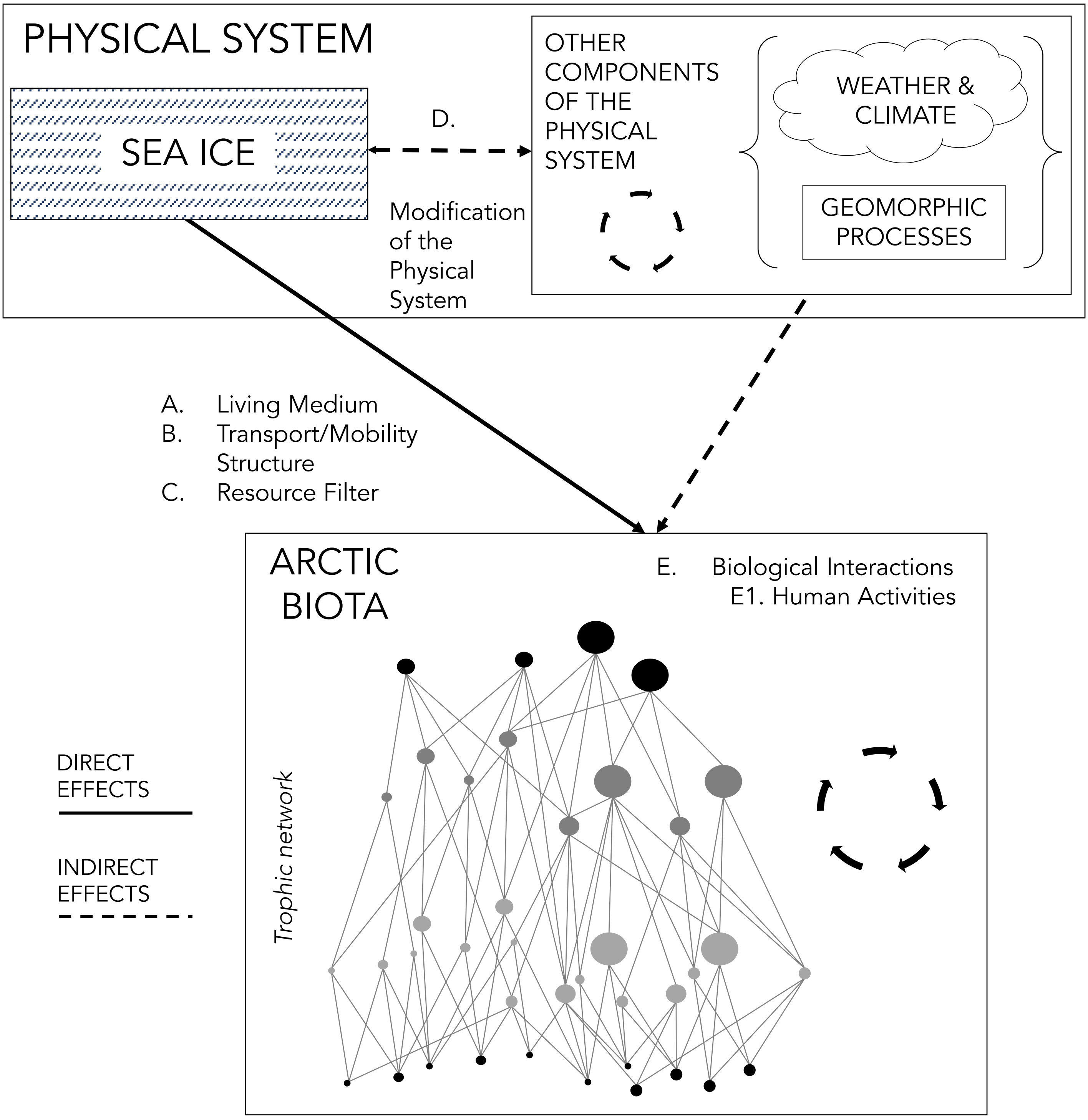


**Figure 1: Arctic Sea Ice *(ASI)* effects on Arctic biota.** <u>*Direct*</u> (**continuous line**): *ASI* modifies Arctic biota's life history events, acting as a ***(A)*** living medium [44; this feature], ***(B)*** transport/mobility-affecting structure [17, 21, 25; this feature], or ***(C)*** resource filter [26; this feature]. <u>*Indirect*</u> (**discontinuous line**): *ASI* affects Arctic biota through chains of events, normally involving ***(D)*** physical system modification [29-31; this feature] and/or ***(E)*** biotic interactions [35-39; this feature], which include ***(E1)*** human activities [41, 42; this feature], or through combinations of *Direct* and *Indirect Effects* (<u>*Compound effects*</u>, see text). *Bidirectional arrow* in ***D*** indicates feedbacks between *ASI* and *Other components of the physical system*, which can modulate *ASI*'s *Indirect Effects* on Arctic biota. *Arrow cycles* indicate possible interactions within *Other components of the physical system* (e.g. *ASI* affecting climate, which in turn affects geomorphology, which indirectly affects Arctic biota) or *Arctic biota* (e.g. *ASI*'s triggered trophic chain responses).