Title: Humanity's redistribution of global biomass flows

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One-sentence summary: Human activities are drastically altering the flows of biomass across Earth, with anthropogenic transport of biomass now far exceeding all long-distance biogenic biomass flows combined.

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Abstract: The biosphere is connected by flows of organic material (biomass), through biogenic (e.g., animal migration) or anthropogenic pathways (e.g., trade). We argue that humans have drastically altered Earth's biomass flows by disrupting animal movement, directly transporting biomass and creating novel biotic pathways. In 2023, transnational anthropogenic transport of biomass through trade far exceeded estimates of all long-distance biogenic biomass flows combined. Human population growth and consumption typically drive anthropogenic flows across longitudes, whereas biogenic flows follow seasonal (typically latitudinal) or local gradients in resources, as individuals spill over from areas of higher to lower resource availability or actively move towards high resource availability. Shifting flows affect organic waste and nutrients, change resource availability to local hunting and fisheries, and disrupt fundamental ecological and evolutionary processes.

Main Text: Flows of non-fossil organic matter (biomass) connect the global biosphere, shaping the distribution of life and its residues (*1*, *2*). Such flows occur when animals follow their resources, and the consequent redistribution of biomass can shape nutrient cycles at a range of scales (*3*, *4*). Resource biomass fundamentally supports that of consumers across trophic levels (*5*) and the ratio of predator to prey biomass is a critical determinant of attack rates, food-web structure and stability (*6*, *7*). Since biomass is also the source or food for humans and livestock, and plant biomass provides fuel and construction materials (*8*), any change to biomass flows will be as fundamental to socioeconomic systems as it is to ecosystems.

Here, we synthesise evidence that human activities cause a global redistribution of biomass by disrupting existing pathways of animal movement and directly or indirectly generating novel pathways. We highlight that human transport of biomass now far exceeds that of other animals, and that the socioeconomic factors governing the direction of this movement and the distribution patterns it generates differ from the factors governing biogenic pathways (e.g. climate, productivity). We leverage recent estimates to compare the transport of organic matter by humans vs. that by other animals and argue that this change critically impacts source and sink ecosystems and the people that depend on them.

While the processes are different, both anthropogenic and biogenic flows transport the same currency of biomass. Combined with abiotic flows, which themselves are subject to anthropogenic environmental influences (e.g. soil erosion via wind or water (*9*), loss of biomass to the atmosphere through burning (*10*) or wind or water transport of pollen (*11*), plankton (*12*) and detritus (*13*)), anthropogenic and biogenic flows affect the local biomass stock, i.e., the net amount of organic matter at a given site at a given time. The balance between biomass locally produced and introduced vs local consumption (including consumption by decomposers) in turn determines the local accumulation of organic residues in the form of waste, nutrients and other environmental externalities.

We begin by synthesising the scale of long-distance biogenic flows (e.g., migration) across animal taxa, then compare them with anthropogenic (e.g., trade) flows. We subsequently examine human disruption of the timing and flow of existing biomass transport pathways by animals, through disruption of movement patterns and changes in biodiversity. We follow by highlighting that anthropogenic flows follow shifting patterns of human population density, economic activity and consumption (*8*, *14*), rather than gradients of resource availability, which drive biogenic flows. While anthropogenic flow can be thought of as the movement of resources to fulfil population needs, it contrasts with biogenic fluxes by exhibiting vastly different per capita import and consumption rates among human populations (*15*). This economic influence can decouple resource consumption from human population size (*16*), and results in the sedimentation of biomass (through waste and nutrient accumulation (*8*)) due to harvest inefficiencies or when the ratio of consumption to need increases above one (*17*, *18*). We highlight recent evidence that this accumulation can occur in either source or sink locations, due to consumption and the externalisation of environmental impacts. In addition, this direct redistribution of biomass creates novel resource gradients, which we argue frequently precipitates the flow of organisms (biogenic flows) through passive diffusion or directed movement along these gradients. We provide examples of such novel biogenic flows as evidence of widespread indirect human impacts on nature's own distribution of organic matter. Finally, we explore the social and ecological impacts of the global redistribution of organic matter.

The scale of biogenic biomass flows

Biogenic flows relate to the movement of mobile (and for the purposes of this comparison, non-human) animal consumers through two processes. The first is essentially passive diffusion: analogous to the movement of abiotic resources, organisms spill over from regions of high resource concentration and population growth to the surroundings (*19*, *20*), thereby reducing spatial differences over time. Such movement typically occurs over scales of a few kilometres, limited by the dispersal ability of individual organisms. An outcome of these 'mass flows' from resource sources to sinks is that local biomass (of species and individuals) in sinks may vastly exceed what would be sustained by the local resource base (*1*, *21*), as areas with plentiful resources subsidise the biomass of consumers in neighbouring areas (through processes known as mass effects (*22*) or trophic subsidies (*23*)). The second type of movement reflects individuals actively moving towards regions of high resource concentrations. Such flows of species and individuals move up resource gradients to maximise their intake (*24*), and thus runs counter to that of passive abiotic diffusion. They are observed from smaller spatial scales, in the active foraging of individuals (*25*), to larger scales in patterns of seasonal migration (*26*), which tend to track resource availability (*27*). Combined with the response of organisms to each other and the resources they transport, animal movement is thus an important modifier of the nutrient and biomass landscape (*28*).

The scale of biogenic flows is massive. Each year, billions of animals move across the planet in pursuit of improved foraging conditions, safety, and reproductive opportunities (Fig. 1). In the absence of formal quantification of migratory animal biomass across taxa, we synthesise available evidence and best-guess estimates to indicate the scale of long-distance migrations (Fig. 2). Among the longest migrations are those undertaken by an estimated 1,855 migratory bird species (one in five extant bird species (*29*)). More than 2 billion passerine birds breeding in the Palearctic regularly migrate to sub-Saharan Africa, to depend on local resources during hibernation (*30*). Moreover, some 5 billion birds – comprising more than 700,000 tonnes of biomass – annually migrate across North America to exploit seasonally-available resources (*31*). Since the Americas flyway is one of the three major flyways globally, a rough estimate suggests that bird migration moves 2.1-3.4 million tonnes of bird biomass annually. The ecosystem impacts of this movement are considerable, as birds can transport significant quantities of nutrients. For example, seabird excretion globally moves 591,000 tonnes of nitrogen and 99,000 tonnes of phosphorous to land per year (*32*), far outpacing that of anadromous fish, which move 5,600 tonnes of P from sea to land (*4*).

Among mammals, migration is widespread in both flying and non-flying families – generally with the intent of enhanced access to forage. Mammal migration has proven exquisitely fine-tuned to dynamic landscapes with seasonal changes in forage, snow, and drought (*33*). Consequently, land megafauna is estimated to move nutrients over 16,000 km^2 per year, while whales move double that amount across the world's oceans (*4*). A rough estimate of current terrestrial mammal migratory biomass, based on the estimated number of individuals (*34*) and each species' mean body mass (*35*, *36*), would be 105,860–525,841 tonnes (Fig. 2). Not only is this biomass an order of magnitude below that of birds, but the distances are also typically much smaller – though some terrestrial mammal migrations can reach upwards of 3,000 km (*36*). However, marine mammals transport significant biomass; a 2001 estimate of whale biomass (*37*) totalled just under 16 million tonnes, exporting 60,138 tonnes of carbon from the euphotic zone each year. Although this estimate included two taxa with variable or population-specific migratory status, the seven migratory taxa included comprise species that cross enormous distances, such as the Minke whales, which migrate between the Arctic and Antarctic (*38*).

Most reptiles (*39*) and amphibians (*40*) migrate short distances of just a few kilometers. However, an exception to these generalizations is marine turtles, which can migrate hundreds to thousands of kilometers (*39*). Although we are unaware of any syntheses of the abundances or biomass of migratory marine turtle species, a synthesis of population trends presented data on nest counts at the beginning of 134 time series of turtle management units (*41*), which (assuming three nests per female, a three-year remigration rate and 1:1 sex ratio) could lead to rough estimates in the tens to hundreds of thousands of tonnes of biomass (Fig. 2).

Estimating the scale of migratory fish biomass is complex, with the biomass of mesopelagic fish being a source of debate (*42*), and the migratory status of many species still being uncertain. Nevertheless, to avoid ignoring these taxa, we draw on a recent estimate of total biomass of fish large enough to be targeted by fisheries (including targeted invertebrates such as squid). This estimate amounts to 1.1 billion tonnes of large, targeted species, out of 4.7 billion tonnes of fish total. Around 2.5% of fish species are known to be migratory (*43*), suggesting that the total migratory fish biomass could fall within the range from 10s to low 100s of million tonnes (Fig. 2). This includes the tunas and related species, which can migrate long distances (and have an estimated biomass across 26 populations of 8.43 million tonnes (*44*), and anadromous fish such as salmon (which are a key transporter of both nutrients and contaminants (*45*)).

These spectacular vertebrate migrations are joined by less visible invertebrate migrations that are as massive as they are ecologically influential, with dramatic consequences for food webs, nutrient transport, pollination, and infectious disease (*46*). Each year, some 3.5 trillion insects (3,200 tonnes of biomass) migrate over a 300km stretch of the southern United Kingdom alone (>105m (*47*)). An estimated 39.6 million diurnal insect migrants arrive in spring in Cyprus via the Karpaz peninsula – suggesting that 6.9 billion insects cross the Mediterranean from 600km of Middle Eastern coastline (*48*). Radar data from China have revealed that 15-16 billion insects (21-26 tonnes of biomass) overfly each square kilometre. When diurnal insects are included, this translates to as much as 50,000 tonnes of insects flying over an area 600km in diameter (*49*). Extrapolating the UK and China numbers to the ice-free land area of Earth would suggest total global insect migration in the order of 0.44-3.5 billion tonnes per year, and others have hypothesised that the number of individual insects involved in seasonal migrations may even be as high as $1 \times 10^{15}–10^{16}$ globally (*46*). Converting this figure to a rough estimate of biomass using mean body masses from the UK and Chinese studies would suggest a range of $9.14x10^{5}– 1.62x10^{7}$ tonnes of migratory insect biomass globally (Fig. 2).

Importantly, the amount of nutrients being moved in insect bodies is equally staggering: spring migrations of over a billion individuals of a single moth species (the Bogong moth, *Agrotis infusa*) transport 7.2 tonnes of nitrogen and 0.97 tonnes of phosphorus up to 1000km and above 1500m into the Snowy Mountain region of Australia (*50*). There is thus no doubt that animal movement is a key biogenic pathway for redistributing organic matter and the nutrients it carries globally.

To our knowledge, there are no estimates of the migratory biomass of marine invertebrates, even within phyla. The global biomass of Cnidarians is estimated to be in the range of 100-130 million tonnes of C (*2*, *51*), which would be tripled as dry weight (*52*), and of these, jellyfish (Medusazoa, around 36% of species (*53*, *54*)) appear to be capable of active movement during their adult stage, sometimes over great distances (*55*–*57*). Cephalopod biomass has been estimated at 193-375 million tonnes (*58*), and a large fraction of these may be migratory (*58*; Fig. 2).

Among decapod crustaceans, movement speed is strongly correlated with body length, though penaeid shrimps and prawns are particularly mobile for their body size (*59*). Decapods comprise 15-25% of micronekton biomass (*59*), with a subset of decapods undertaking horizontal migrations, seasonally or for spawning (*60*). Although global estimates of micronekton biomass are contentious, a size-spectrum model estimated the global micronekton biomass to be 2.82 Gt, including 0.96 Gt of migrant mesopelagic organisms ((*61*, *62*); Fig. 2). These figures suggest that migrations of crustaceans (many of which may be only in the order of few kilometers), may carry a significant amount of biomass.

The scale of anthropogenic biomass flows

Biogenic biomass flows are now more than rivalled by anthropogenic flows. The global biomass stock of wild mammals (≈0.007 Gt C) is far surpassed by that of humans (≈0.06 Gt C) or livestock (≈0.1 Gt C), and that of wild birds (≈0.002 Gt C) is surpassed by domesticated poultry (≈0.005 Gt C) (*2*). This enormous contribution of humans and their livestock to the global distribution of animal biomass stock is itself significant, but the transport of plant and animal biomass by humans also represents a major flow (Fig. 2). Human consumption of net primary productivity varies spatially, and is maintained by resource transport (*63*). These flows occur as living resources, or their residues (in the form of crops, timber, fish, etc.), are traded and moved to satisfy human consumption.

In 2023, a total of 2 billion tonnes of crops and animal products were exported from their nations of origin (*64*). Of this total, some 200 million tonnes consisted of wheat crops alone. Adding the volumes of forestry products (728 million tonnes, assuming a volume to biomass conversion of 1.48m^3 per tonne, equivalent to wood chips/sawdust) and live animals (1.9 billion animals in 2023, with an average weight of 195kg for stock animals (*2*, *64*, *65*)), we may calculate that some 3.16 billion tonnes of terrestrial biomass was transported between countries in 2023. In the same year, world trade in fish and fisheries products was estimated at 65 million tonnes (*66*). Humans also transport their own biomass, with OECD countries recording 6.5 million permanent migrations in 2023 (*67*), totalling around 380,000 tonnes (Fig. 2).

Although we are unaware of any synthesis of global large-scale animal movement rates (but for a subset see (*4*)), the above estimate of human trade across borders is around 240 times higher than our very highest back-of-envelope estimate of global migratory insect biomass and over a thousand times our highest approximation of migratory bird biomass (Fig. 2). Overall, human cross-border trade transports between two and four times the biomass of existing rough estimates of all long-distance migratory animals combined (Fig. 2). If we focus on terrestrial biogenic flows, which (besides insects) are better characterised in terms of distance and biomass than many of the significant marine pathways, trade of land-sourced biomass is 150-1000 times higher than biogenic migration of biomass (Fig. 2). In addition to these cross-border transactions, domestic trade can also move large quantities of biomass across considerable distances, though estimating biogenic movement at such smaller scales for comparison would be extremely difficult. To illustrate human domestic trade, already in 2002, total domestic transport of food in the UK amounted to an estimated 50 billion ton-kilometres (*68*). Thus, it is likely that human trade in 2023 far exceeded the natural long-distance movement of biomass by animals (Fig. 2).

Disruption of existing biogenic flows

The growth in human biomass transport has been accompanied by the simultaneous disruption of biogenic flows, thus further tilting the balance between the two. Human-driven environmental changes have altered biomass flow through animal movement at a range of scales (Fig. 3).

At the largest scale, global migration patterns are rapidly changing, causing major concerns of both direct and indirect effects on ecological communities (*26*). Most obviously, biodiversity loss influences the net numbers of animals able to migrate. For example, the North American avifauna has suffered a net loss of some 3 billion birds during the last half-century, amounting to about one-third of 1970 abundances (*69*). World-wide, an estimated 132 (around 7%) of migratory birds are globally threatened (*70*), with this number growing to 17% if extinct species are included (*71*), and only 9% are adequately covered by protected areas (*72*). Again, changes to the more spectacular migrations of the megafauna are joined by changes to the meso- and microfauna. Climate change and other anthropogenic drivers alter the area over which insects migrate (*73*), as well as their timing and abundance (*46*).

Climate change poses a particular challenge to animal migration, as it also changes the timing of seasonal events. In general, migrating animals aim to track seasonal variation in food across space (the "surfing the green wave" hypothesis (*74*)), such that regional unevenness of climate change may disrupt migration through different warming rates in breeding vs wintering grounds (*75*). Among birds, climate change, habitat modification and changes in food availability are causing changes in hibernation habitats (*76*) and patterns (*77*, *78*). For one of the main routes of bird migration through the US, the Central Flyway, the passage dates have advanced consistently by some 0.6 days/decade. Nonetheless, the passing birds fly through a different set of temperatures and landscapes at another level of spring greening than before. Thus, resource availability during migration has changed, whereas adjustments to the timing of migration have not compensated for the effects of a change in climate (*79*). Similar mismatches have been observed in the marine megafauna, where long-lived blue whales (*Balaenoptera musculus*; Fig. 1) (*80*), fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) (*81*) are struggling to match the timing of their migration to increasing annual variation in food availability.

The seasonality and predictability of resources is also a key determinant of animal movement generally (*82*), with consequences that permeate across scales of biological organisation, from genes to communities (*83*). The timing of biomass subsidies (particularly their asynchrony with internal resource availability) can be important for determining their value to recipient communities (*84*). By disrupting spatial and temporal patterns of resource availability, human activities can alter the eco-evolutionary drivers of animal movement (*82*). For instance, trade of produce has seasonal patterns (*85*), with imports and exports of commodities such as fresh fruits being inversely correlated across hemispheres (*86*). Consequently, the removal of biomass for export and the consistency of import created by economic globalisation reduce the magnitude of seasonal changes and increase the predictability of resource availability, thereby influencing animal behavior. For example, Iberian populations of the white stork (*Ciconia ciconia*) have switched from being migratory to engaging in year-round nesting due to the continuous food availability in landfill sites (*87*). Thus, the predictability of anthropogenic resources can alter selective forces or attract species to suboptimal habitats, thereby generating ecological traps (*82*).

Within continents, changes in land cover have caused loss and fragmentation of habitat, which has drastically reduced mammal movements in areas with a high human footprint (*88*). Among terrestrial mammals, most mass migrations occur in response to the seasonal and shifting patterns of greening vegetation over grasslands (Fig. 1; (*34*)). Of 24 large-bodied ungulates migrating in aggregations, mass migrations for six species are currently extinct or unknown. Most remaining migrants (nine species) occur in six locations in Africa, with Eurasia and North America containing six and four remaining mass migrants, respectively (with caribou/reindeer *Rangifer tarandus* occurring in both regions). All migrants have declined in abundance, with exceptions in the Serengeti-Mara Ecosystem, Sudan, and some caribou populations. Principal threats include overhunting and habitat loss from livestock, agriculture, and fencing that excludes animals from forage or water (Fig. 3; (*34*)). Importantly, these recent disruptions should also be put in the context of longer-term, anthropogenic changes to the migratory fauna, including the late Quarternary extinctions of megafauna (*4*).

Disruption of terrestrial migrations by fencing and habitat discontinuities parallels that of aquatic migrations by human barriers to flows (*89*). Some of the largest aquatic biomass flows have been cut by damming nearly all major rivers (*90*) – a development which continues unabated (*91*).

At smaller spatial scales, subsidies of organic material as organisms and detritus are crucial determinants of the functioning of freshwater ecosystems (*92*, *93*). Thus, environmental changes in hydrology, temperature, species distributions (including invasions) and riparian land use can alter these flows (*94–97*). Conversely, human impacts on aquatic ecosystems, floodplains and riparian habitats influence the flow of subsidies in the opposite direction, from water to land (*98*). Such flows involve the emergence of aquatic insects, the timing of which can be critical for sustaining insectivorous bird populations during reproduction (*99*).

The novel landscape of anthropogenic flows

While both biogenic and anthropogenic flows are currently altered, two key differences distinguish the two: First, whereas biogenic flows largely follow seasonal fluctuations in productivity across latitudes (between North and South), anthropogenic flows occur between East and West (along longitudes; Fig. 1). Second, the spatial distance of transport equals or exceeds the migration paths of even flying animals such as birds (Fig. 1).

A key driver of the direction and distances of anthropogenic flows is economic globalisation, which has caused resource consumption to be increasingly separated spatially from production (*100*), thereby increasing the distance over which biomass travels (Figs. 1,3,4). For example, recent estimates suggest that China is responsible for nearly 12% of the consumption of human-appropriated net primary production, consuming biomass at a rate of 1.75 petagrams of carbon per year, making it the highest net importer. Yet, the principal sources of imports to China are Latin America and the Caribbean (*100*), thus creating a massive flow of biomass from west to east (Fig. 1,4). As a stark illustration of the indirect redistribution of biomass, 86% of global deforestation can be attributed to crop and cattle production (*101*), and roughly a quarter (26%) of the approximate 5.5Mha of forest loss per year can be attributed to international demand (Fig. 2; (*102*)). The bulk (87%) of this export occurs to countries that either exhibit decreasing deforestation rates or increasing forest cover, particularly in Europe and Asia (Fig. 4). About a third of the net forest gains is thus offset by deforestation elsewhere, amounting to an indirect global shift in forest biomass stocks (Fig. 4; (*102, 103*)).

Trade in marine biomass has also expanded in both volume and distance. Over the past 25 years, aquatic foods have become increasingly globalized, with the share of production exported increasing by 40% (*104*). During the same period, global consumption increased by 19.4%, with several regions becoming increasingly reliant on aquatic foods sourced from other regions (*104*). Asymmetric flows occur from net exporter countries (e.g. in Asia and South America) to net importers (North America and Africa), but the selection of species generates a disproportionate net flow of species at lower trophic levels, with species at higher trophic levels moving in the reverse direction (*105*). Thus, anthropogenic flow of seafood does not shift biomass at random – rather, market forces globally redistribute the ecological impacts of losing biomass at particular trophic levels (*105*).

More generally, rather than diffusion up or down productivity gradients, as occurs with biogenic flows, the flow of goods occurs along gradients of population density and/or economic development at a range of scales (Fig. 4). Globally, trade in resources typically occurs from nations with lower to higher GDP per capita (Fig. 4). This spatial outsourcing of production shifts environmental degradation to low-income countries, driven by demand in high-income countries (*102*, *105*). For instance, it is estimated that >0.50 Tg y-1 of P accumulation in soil and freshwater is driven by agricultural trade (*106*)).

Within nations, the production of food and fibre typically occurs in regions of low population density and, thus, large volumes of biomass are transported from rural to urban populations (*68*). As a result, waste products and fertilising nutrients accumulate in rural production hubs or neighbouring waterways, driven by urban demand nationally or internationally (*107*). For example, in India, the import demand from six states alone is met through net nutrient application of 1140 $GgNyr^{-1}$ and 330 $GgPyr^{-1}$ to produce that biomass, leading to nutrient surplus in the production regions (*108*).

In addition to the indirect export of nutrient waste accumulation, transport of biomass in food shifts key macro and micronutrients over far greater distances than their natural diffusion, potentially driving nutrient depletion in export locations and accumulation in import locations (*109*). For example, recent estimates suggest that developing regions such as sub-Saharan Africa, Latin America and Southeast Asia were net exporters of 5.8 Mt P through agricultural trade between 1970 to 2017 (54% for non-food markets), increasing deficits of soil P in regions with already low soil P reserves (*110*). Thus, organic waste may parallel nutrient flows, accumulating in areas of wealth, leading to nutrient enrichment and directional waste streams (*111*).

Biogenic flows respond to novel resource gradients

In addition to the direct transport of organic material or disruption of natural biogenic flows, humans indirectly generate biogenic biomass flows by altering the nutrient gradients that can drive them. Although many examples of these novel biogenic flows occur over short spatial distances, it is their global ubiquity that underpins their importance. While our focus here is on biomass rather than nutrients, changes to the nutrient landscape influence biogenic flows of organic matter. For example, human addition of e.g., nitrogen equals or surpasses the nutrient flows from all prehuman/natural sources (*112*, *113*). Direct trade of phosphorous and trade in commodities resulting from phosphorous addition is massive (*114*). The prehuman reactive phosphorus flux to the ocean is estimated to have ranged from 0.7—4.8 Tg/yr (*115*). The global anthropogenic P load to freshwater systems from both diffuse and point sources is estimated at 1.5 Tg/yr, 38% from agriculture (*116*). For nitrogen, the impacts are equally drastic: human activities currently contribute about half of all fixation of reactive nitrogen annually (*112*), and human land use further alters biological fixation of N, significantly influencing global cycles (*117*). Since biogenic flows tend to occur up or down resource gradients and be influenced by the extent and predictability of resource availability, changes in this predictability affect animal movement – which further shifts the flow of nutrients (*82*) at a range of scales. Thus, the novel resource gradients created by human transport of nutrients, biomass and organic waste are creating new types of directed biogenic flows.

A defining period in food production has been the green revolution, resulting in continued increases in land-use intensity and human appropriation of net primary productivity across the globe (*118*). Between 1961 and 2014, a 137% increase in inputs allowed humanity to triple global food production with only a 10% increase in growing area (*119*). This unprecedented increase in productivity of human land use created stark contrasts in resource availability relative to surrounding natural areas, modifying cross-ecosystem biomass flows (*120*) and driving spillover of agriculturally-subsidized organisms across the boundary into natural systems (*121*), alongside the spillover of agricultural fertilisers themselves (*122*).

In terms of mass flows down resource gradients, spillover of organisms from areas of high resource availability to surrounding regions is a key characteristic of modern landscapes (*20*, *123*). Since local resource concentrations may create high abundances of individuals, a subset of them will move to the surrounding landscape, potentially augmenting local densities of either pests (*124*), predators (*125*) or both (*123*).

In addition to mass flows down resource gradients, active movement of individuals towards regions of high resource concentrations generates flows at smaller spatial scales through active foraging of individuals, whereas flows at larger spatial scales reflect patterns of seasonal migration (*26*). Active and mass flows and their impacts are likely to correlate positively with the contrast in productivity between coupled habitats (*20*, *92*, *126*); a relation for which there is both theoretical (*127*, *128*) and empirical support (*92*).

Social, economic and ecological impacts of biomass redistribution

Above, we have shown that anthropogenic and biogenic biomass flows follow fundamentally different routes and drivers (Fig. 1), and that biogenic flows have also been altered and generated by humans (Figs. 3). These changes result not only from changes in human trade or anthropogenic barriers to animal migration, but from the complex interplay between anthropogenic redistribution of resources and biogenic responses to these changing resource patterns. As such, the consequences are manifold, and the impacts will typically span across economic, social and ecological systems.

From a social and economic perspective, the new regime of global resource flows has a key consequence: with economic development, humanity outsources extractive resource use (Fig. 4). Thus, the transport of biomass and its derivatives at a global scale mean that biomass (e.g., in forests) is depleted in regions widely different from where it is consumed (Fig. 4; (*102*, *103*)). In other words, anthropogenic biomass flows allow the overconsumption of living resources far from the consumer, thereby imperilling the ecosystem services available to entirely different human communities and societies (*129*).

Altered migratory species biomass and diversity can also carry economic costs. For example, birdwatchers are the largest and fastest-growing ecotourism market, with considerable potential to benefit local communities (*130*) – and bird movement and migration contributes to this industry. A study in Pennsylvania, USA, estimated that a single vagrant Black-backed Oriole (*Icterus abeillei*, an endemic to Mexico) stimulated travel activity worth $223,000 USD or about $3,000 per day over 67 days (*131*). Thus, barriers to biogenic biomass flows may harm economic activities such as hunting, fishing and non-extractive uses such as tourism. The values at stake are substantial. As a case in point, the value of global safari tourism – which partly targets spectacular animal migrations – was estimated at USD 33.1 billion in 2024 and projected to grow from USD 36.64 billion in 2025 to reach USD 60.91 billion by 2030 (*132*).

Concomitantly, massive increases in human trade and transport have brought unprecedented opportunity for the spread of new species to regions that they could not reach before. The resulting problem of invasive species (including agricultural pests) causes annual losses of over 423 billion USD (*133*). At the smaller scale of landscapes, spillover of species over novel resource gradients (e.g., among land uses) can influence the abundance of vertebrate pests (*134*) and impact invertebrate crop-pest densities (*135*) and the resulting need for pesticide expenditure (*136*). These detrimental impacts can in some cases be offset by the movement of species that contribute positively to people, such that the mosaic of human land uses can generate a complex landscape of trade-offs among costs and benefits derived from mobile species (112).

The socioeconomic impacts of changing biomass flows may disproportionately affect Indigenous Peoples and Local Communities who have long associations with migrating animals. For example, human activities such as land use, mining, transport and construction influence caribou/reindeer movement and migration, impacting Indigenous Peoples in Sweden and Canada. These peoples have long cultural connections with caribou (*138*, *139*), and migrating populations are an important traditional food contributing to their food security (*140*). The loss of connection with such cultural keystone species can cause a series of biocultural feedbacks, potentially impacting social structures, knowledge generation and transmission, and peoples' connection to place (*141*).

Similar issues pertain to Indigenous Peoples whose food security is impacted by changing salmon migration paths or frequencies (*142*), a phenomenon that is repeated globally. Prior to European settlement, 160–226 million kg of salmon migrated each year up the rivers of the US Pacific Northwest. Today, the total biomass of spawning salmon in the Pacific Northwest is estimated to be only 12–14 million kg. Consequently, rivers of the Northwest receive just 6%–7% of the marine-derived nitrogen and phosphorus they once received from the abundant salmon population (*143*). At the same time, this has depleted local fisheries, causing economic losses and damage to local culture (*143*). In fact, surplus feed from salmon aquaculture attracts a range of fish species, which are then vulnerable to disease, such that novel biogenic flows to this anthropogenic resource serves as an ecological trap for wild fish (*144*).

Beyond the socioeconomic impacts, changes in flows will have drastic effects on local ecosystems. Seasonal migration allows the persistence of much larger populations of wildlife than if they did not move (*145*). For a resident population, the population size is typically set by conditions during the locally leanest season, but by following patterns of productivity shifting in space and time, the population can avoid the wave trough of low densities. Once disrupted, these strategies can have impacts that propagate across food webs. For example, declines in migratory birds may pose a serious threat to the health of our forests and farmlands. A back-of-an-envelope calculation (*146*) suggests that that more than 30,000 tonnes of migratory songbirds annually migrate between Latin to North America – consuming at least 3,000–10,500 tonnes of insects per day. How declining predation from dwindling migrations will affect local insect populations is virtually unknown – as is the opposite question of how migrations of dwindling insect populations (*147*, *148*) will affect bird populations (but see (*149–151*)).

From the perspective of the species themselves, changes to cross-habitat movement or cross-continental migration will influence the community in which the species are embedded, altering the availability of interaction partners (*26*, *152*, *153*). Everywhere individuals flow, they alter local community structure, dynamics, and ecosystem function (*26*). In doing so they temporarily provide prey to local predators, or forage on local resources themselves, and thereby contribute to the local nutrient and energy cycles. Along their route, they provide vectors for hitchhiking organisms, from parasites to plant propagules (*26*). Birds alone may serve as predators, pollinators, scavengers, seed dispersers, seed predators, and ecosystem engineers in whatever community they enter (*154*). In other words, in a world characterised by frequent migration, we will see local communities entirely different from those expected on the basis of the local resources (*26*) – whereas a world with less migration will be more strongly shaped by the site-specific resource base.

Finally, changes in flows will also affect ecosystem functioning and dynamics. Spatial subsidies of resources can differentially benefit trophic levels (*92*) and alter the importance of predation versus resource availability as drivers of food web dynamics (*155*). Changes in the availability of biomass at lower trophic levels through nutrient and detrital enrichment may be destabilising to food webs (*156*), whereas the spatial pattern and quality of resources can alter the distributions of mobile consumers (*157*) and the optimal choice of resource (*158*), which together can shape the structure and functioning of entire food webs (*156*, *159*, *160*).

Conclusions and future directions

Above we have outlined how humanity’s redistribution of biomass flows at a range of scales weave into each other, causing drastic impacts spanning economic, social and ecological spheres. Yet, the management of these changing patterns is challenging, as the range of biogenic and anthropogenic flows typically spans many national legislations and wide sociopolitical gradients (*146*). This complexity is exacerbated by the number of policy domains driving these impacts. For example, primary industries, trade, infrastructure and conservation typically comprise separate legislative portfolios, making a coordinated response particularly challenging, even within a single jurisdiction. Nevertheless, the retention of remaining biogenic flows emerges as a key priority. Key principles include securing seasonal ranges, resource protection, government support of migratory species and minimizing barriers to migrating animals ((such as dams and fences; Fig. 3; (*34*)). While our review has pointed to crucial changes in global biomass flows, it has also exposed critical knowledge gaps. Despite the massive scale of the flows here estimated, many of our estimates were derived on the back of an envelope. Such poor knowledge of processes of global importance seems an untenable *status quo*. Most notable among these is invertebrate (both terrestrial and aquatic) migration, which are possibly the greatest migration biomass but also the most poorly quantified. Yet, for terrestrial insects at least, recent advances in the use of radar data (*46*, *161*, *162*) could be scaled up through global consortia to quantify flows of insect and bird biomass.

Although there is considerable focus on fish stocks, including of migratory taxa, there is uncertainty about the migratory status of many fish (*163*), and global syntheses of existing (and often localised) stock assessments would be valuable. Marine turtle migratory biomass may also be possible to rigorously estimate with existing data, by combining population censuses with species biomass averages.

Although future work is needed to rigorously estimate both biogenic and anthropogenic movement of biomass at several spatial scales, present-day understanding is sufficient to emphasise both the magnitude and impacts of its novel redistribution. We have presented a handful from the many examples where communities depend economically and culturally on migratory species, and these species are known to have important ecological impacts on food webs and nutrient cycles. The impacts of spatial subsidies of organisms and detritus for food webs and their stability are also known well enough to conclude that humanity's redistribution of biomass is having profound ecological impacts alongside the positive and negative, direct and indirect socioeconomic effects of trade.

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Acknowledgments: We are most grateful to Pinja Kettunen for creating Figures 1–3 and to Irene Conenna for creating figure 4. Martin Persson kindly directed us to the key data behind figure 4.

Funding:

European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme, grant agreement No 856506; ERC-synergy project LIFEPLAN (TR)

Swedish Research Council Vetenskapsrådet, Dnr 2023-05118 (TR)

Ministry for Business, Innovation and Employment, programme C09X2104 (JMT)

Ministry for Business, Innovation and Employment, programme C09X2209 (JMT)

Bioprotection Aotearoa Centre of Research Excellence (JMT)

Author contributions:

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Methodology: JMT, TR

Investigation: JMT, TR

Funding acquisition: TR, JMT

Writing – original draft: TR, JMT

Writing – review & editing: TR, JMT

Competing interests: Authors declare that they have no competing interests.

Data and materials availability: All data are available in the main text.

Fig. 1

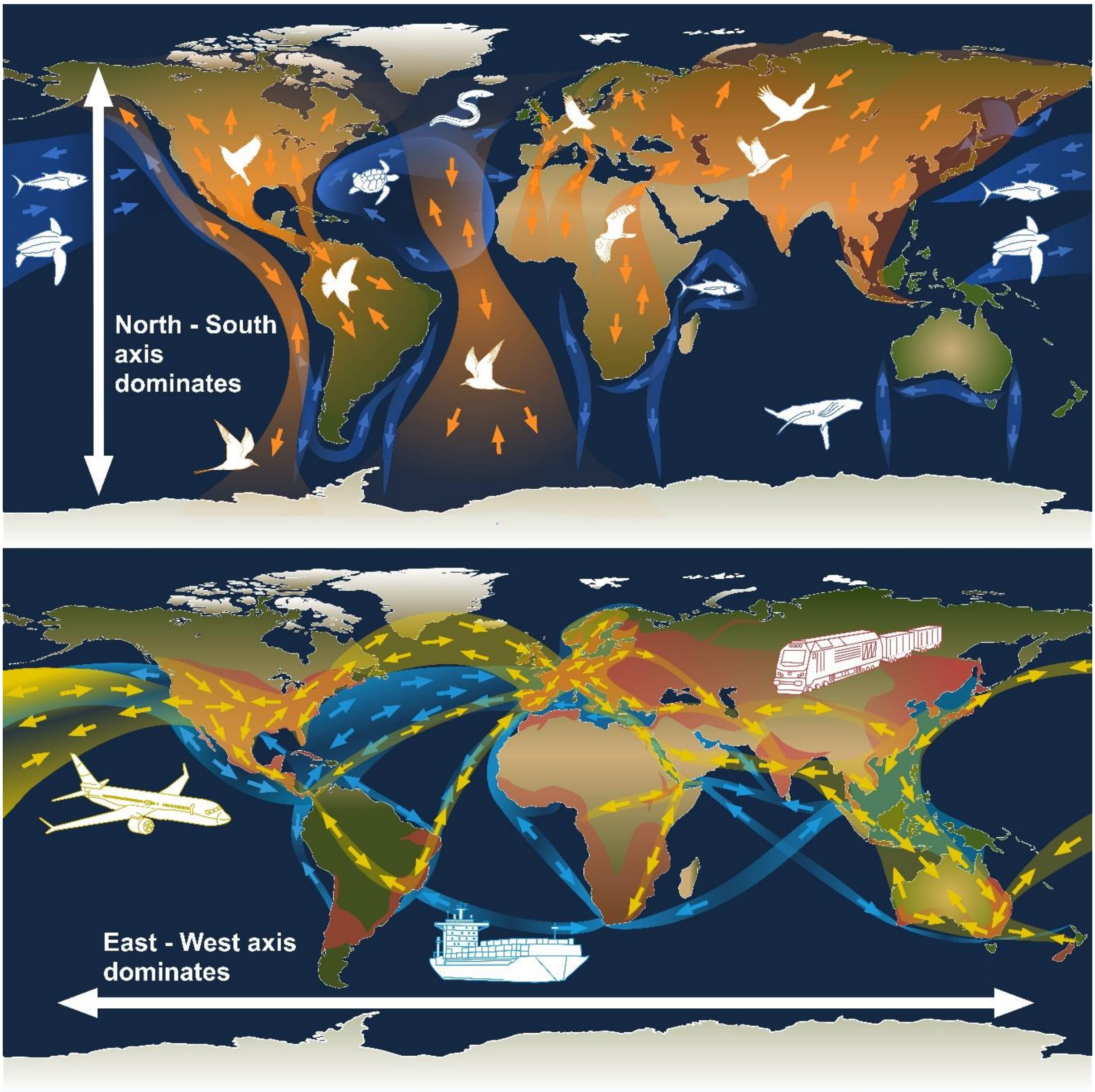

Fig. 1. Global patterns of current biomass flows generated by biogenic processes (top) and anthropogenic transport (bottom). Arrows are synthesised from global maps on key migration routes (*164–176*) and global statistics on transport (*177–180*).

Fig. 2

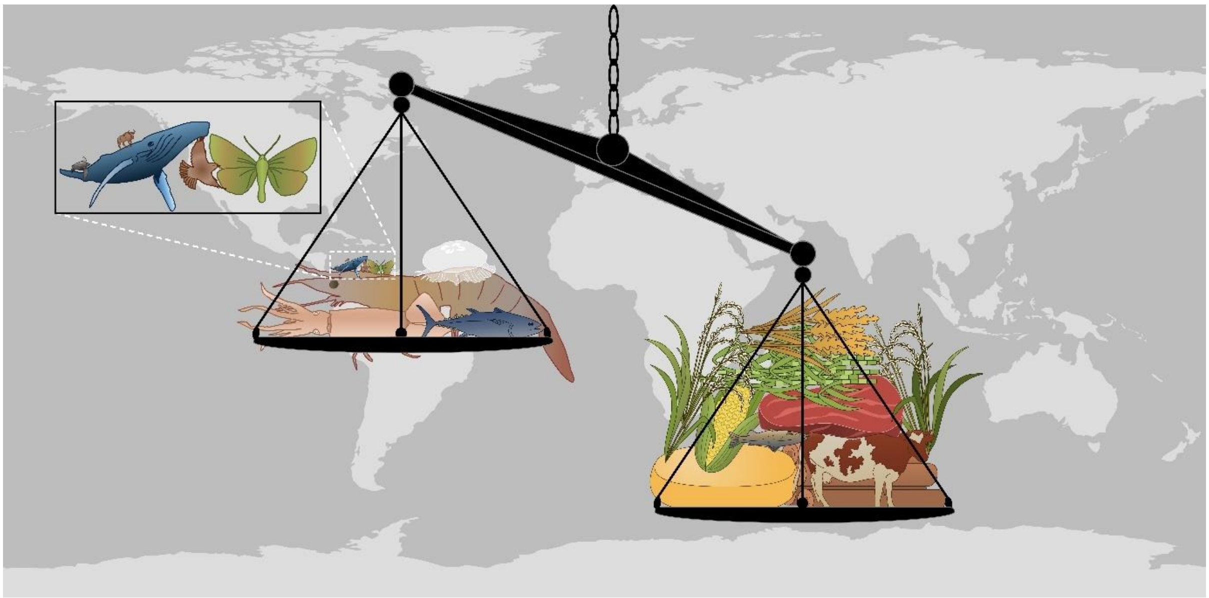

Fig. 2. The current balance between biomass flows generated by biogenic processes (left-hand pan) and anthropogenic transport (right hand pan). The size of each contribution is based on best-available estimates of migratory biomass described in the main text (with sources). Organisms in the left-hand pane correspond to flows of marine turtles, birds, mammals, whales, insects, fish, cnidarians, cephalopods and decapods, respectively, with the insert showing an enlargement of smaller biomass contributions. Goods in the right-hand pane correspond to human trade in fish, crop and animal products, forestry products and live animals, respectively.

Fig. 3. Key changes in biogenic and anthropogenic flow patterns over the past 50 years. The figure synthesises the waning of bird migration and the disruption of migration routes through damming of rivers and fencing of terrestrial regions – as accompanied by a massive growth in human transport.

Fig. 4

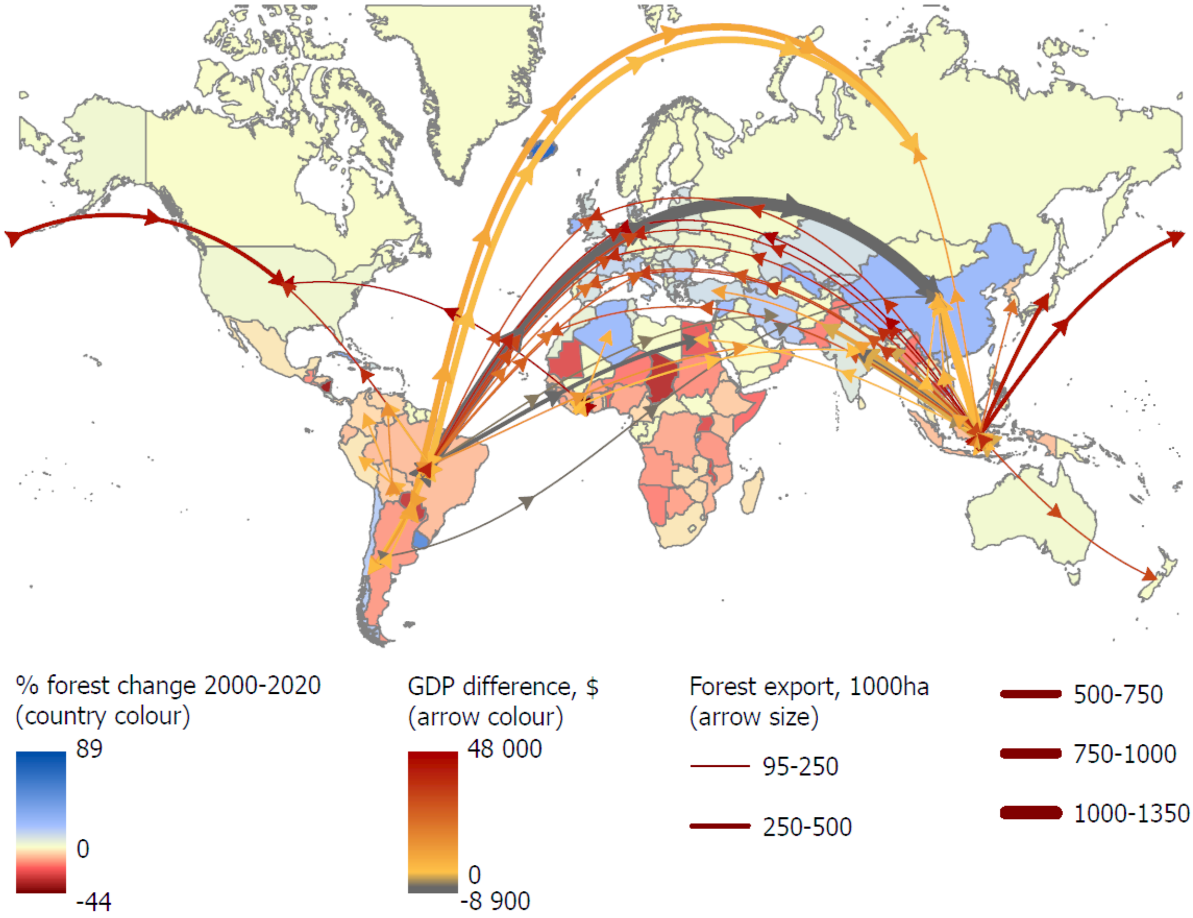

Fig. 4. The outsourcing of forest loss through international trade. Paths show the flow of virtual forests (i.e., forests being converted to other land use types for the production of exported commodities) between countries at different income levels. For each country, the fill colour shows the percent change in forest cover 2000–2020; blue colours signal forest gain, light green no change; red colours loss – see legend in map). Arrows show trade in units of virtual forest, i.e., the area of forest lost due to land use conversion in the exporter countries: the wider the arrow, the greater the trade. Arrows are pointed in the direction of the net receiver (i.e., the country gaining virtual forest). Arrow colour shows the difference in per capita gross domestic product (GDP) between the exporter and the importer countries. Red colour implies that the receiver has higher per capita GDP than the sender; green marks the opposite. For visual tractability, only the 50 largest trade flows are included in the map. Note that most arrows are red, implying that consumption of imported goods in higher-income countries drives forest loss in lower-income countries**,** with the remarkable exception of strong flows to China. Overall, about a third of the net forest gains is offset by deforestation elsewhere, amounting to a global shift in biomass (*102*). Data sources: (*65*, *102*).