

RESEARCH REVIEW

Considering land–sea interactions and trade-offs for food and biodiversity

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Abstract

With the human population expected to near 10 billion by 2050, and diets shifting towards greater per-capita consumption of animal protein, meeting future food demands will place ever-growing burdens on natural resources and those dependent on them. Solutions proposed to increase the sustainability of agriculture, aquaculture, and capture fisheries have typically approached development from single sector perspectives. Recent work highlights the importance of recognising links among food sectors, and the challenge cross-sector dependencies create for sustainable food production. Yet without understanding the full suite of interactions between food systems on land and sea, development in one sector may result in unanticipated trade-offs in another. We review the interactions between terrestrial and aquatic food systems. We show that most of the studied land–sea interactions fall into at least one of four categories: ecosystem connectivity, feed interdependencies, livelihood interactions, and climate feedback. Critically, these interactions modify nutrient flows, and the partitioning of natural resource use between land and sea, amid a backdrop of climate variability and change that reaches across all sectors. Addressing counter-productive trade-offs resulting from land–sea links will require simultaneous improvements in food production and consumption efficiency, while creating more sustainable feed products for fish and livestock. Food security research and policy also needs to better integrate aquatic and terrestrial production to anticipate how cross-sector interactions could transmit change across ecosystem and governance boundaries into the future.

KEYWORDS

biodiversity, food production, food security, land–sea interactions, sustainable development, trade-offs

1 | INTRODUCTION

Population growth and dietary shifts towards greater consumption of animal-protein are expected to increase current human food demand by over 50% in the next 30 years (Alexandratos & Bruinsma, 2012; Tilman & Clark, 2014). Meeting these demands through further intensification and expansion of terrestrial,

freshwater, and marine food production threatens global biodiversity and the structure and function of natural ecosystems (Brussaard et al., 2010). Creeping loss of environmental services from natural habitat destruction undermines the integrity of the human and natural components of our food system (Ostrom, 2009), and poses a huge threat to the food security of millions of people. Thus, there is an urgent need to understand the social-ecological trade-offs from a

variety of development pathways proposed to meet future food demands.

Meeting future consumption demands will require development across all food production sectors. On land, genetic modification, increased waste efficiency, or integrated pest management strategies can close the gap between realized and maximum potential crop yields (Godfray & Garnett, 2014; Godfray et al., 2010; Tilman, Balzer, Hill, & Belfort, 2011). Better fisheries management throughout the global ocean, and advances in aquaculture feed technologies may also allow per-capita fish consumption to increase, while reducing impacts on aquatic resources (Béné et al., 2015; FAO, 2016; Jennings et al., 2016). Yet, the challenge is not isolated to increasing production alone. Improving food security for 800 million people living in hunger worldwide requires tackling barriers to food access (Sen, 1981). Overcoming disparities in access requires vast improvements in gender equity, trade reforms, and natural resource management as highlighted by the United Nations Sustainable Development Goals (FAO IFAD WFP, 2015; United Nations, 2015b). Most solutions, however, continue to focus on a combination of single sector approaches to development—including both aquatic and terrestrial food systems—but largely ignore the human dependencies that reach across multiple sectors and ecosystems.

Interactions among species or functional groups within ecological food webs are widely recognised as fundamental in determining system-wide responses to perturbations (Marzloff et al., 2016; Suttle, Thomsen, & Power, 2007). Here we apply the same thinking to an integrated global food system, with interacting marine, freshwater, and terrestrial sectors (fisheries, aquaculture, and agriculture) burdened by population growth, shifting diets, and climate change. Interactions among food sectors have pivotal roles in the transfer of impacts from one region to another via the disruption of environmental services and trade, or from human adaptation strategies that shift resource use (Warren, 2011). Interactions between fisheries and aquaculture in the marine environment have been the focus of a substantial body of research in recent years (e.g. Arechavala-Lopez, Sanchez-Jerez, Bayle-Sempere, Uglem, & Mladineo, 2013; Natale, Hofherr, Fiore, & Virtanen, 2013; Naylor et al., 2000). Nevertheless, the links and interactions spanning food systems and ecosystems on land and sea remain vastly understudied.

Lack of integration is not surprising given organizational and institutional norms, structures, and incentives that lend to specialised knowledge within disciplines (Viseu, 2015), thus silo approaches to management. Nonetheless, we need a new perspective on sustainable development of the food system that incorporates how development in one sector can affect another. Recent work highlights how links and interdependencies connecting food sectors on land and sea present challenges for sustainable food production (Blanchard et al., 2017). Yet, the full scope of land–sea interactions among food production systems is not understood. To address this gap, we review the suite of interactions connecting terrestrial and aquatic (both marine and freshwater) production systems to highlight connectivity, and discuss the social-ecological trade-offs that result from various intensification strategies (see “Appendix S1” for review

methods). We show that four main pathways link food sectors on land and sea: ecosystem connectivity, feed interdependencies, livelihood interactions, and climate feedback (Figure 1).

2 | ECOSYSTEM CONNECTIVITY

Terrestrial, freshwater, and marine habitats are inextricably linked through the energy, material, or organisms that pass between them (Gorman, Russell, & Connell, 2009). Rivers and streams play a fundamental role in the flow of subsidies across the land–sea interface (Tallis, Ferdaña, & Gray, 2008) and are pivotal in transferring impacts between systems. The asymmetric flow of water from land to sea means changes in habitat structure on land may be of greater consequence for aquatic systems than vice versa (Álvarez-Romero et al., 2011).

Water extraction for agriculture can pose significant threats to ecosystems and human activity downstream (Atapattu & Kodituwakku, 2009). Agriculture accounted for 92% of global freshwater consumption from 1992 to 2005, primarily through irrigation (Hoekstra & Mekonnen, 2012). Upstream water extraction and irrigation schemes reduce water flow otherwise delivered to coastal ecosystems with considerable impact on downstream fisheries. Reductions in lateral flooding and increases in salt-water intrusion limit the capacity for wetlands to support both biodiversity and productive fisheries, and has been a major source of conflict in deltaic areas in

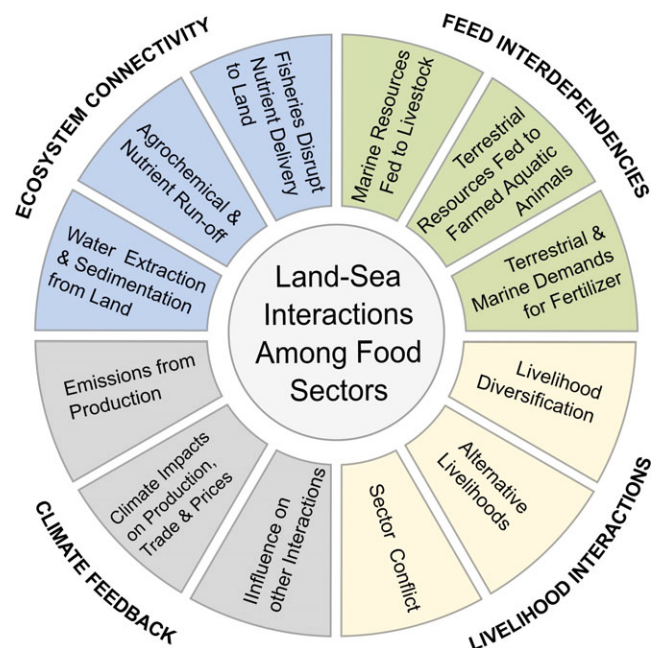


FIGURE 1 Summary of land–sea interactions among food production systems. Ecosystem connectivity, feed interdependencies, livelihood interactions, and climate feedback link aquatic and terrestrial production systems

Asia, Africa, and Australia (Craig, Halls, Barr, & Bean, 2004; Islam & Gnauck, 2008; Lemly, Kingsford, & Thompson, 2000).

Terrestrial farming also influences the structure and function of aquatic systems worldwide through major changes to land-use. Conversions of forests, grasslands or wetlands to grazing or arable land are the most common (Galloway et al., 2010). Changes in vegetative-cover influence hydrological processes such as infiltration, which if decreased, increases surface-run-off and disrupts vegetative nutrient uptake (Galloway et al., 2010).

Hydrological alteration and changes to nutrient loading by crop-livestock systems are the single largest source of disruption to nitrogen and phosphorous flows between ecosystems (Bouwman et al., 2013). Global, regional and local transfers of nitrogen have undergone dramatic transition since the Haber-Bosch process allowed humans to convert non-reactive nitrogen gas to ammonia for use in synthetic fertilisers (Galloway et al., 2003, 2010). Globally, crop systems receive 75% of all reactive nitrogen compounds created by humans. The vast majority of fertilisers applied are lost to waterways and the atmosphere—only 20% of nitrogen delivered to arable land reaches livestock, less than 10% directly contributes to human food. Moreover, on a global basis approximately 85% of nitrogen fed to cattle is lost in manure and waste (Galloway et al., 2003, 2010; Smil, 2002). Manure stored in earthen ponds then leach massive quantities of nutrients into groundwater and waterways, exacerbating nitrogen deposition in aquatic environments (Kato, Kuroda, & Nakasone, 2009; Tilman, Cassman, Matson, Naylor, & Polasky, 2002).

Diffusing into rivers and streams, agricultural run-off is a major driver of biodiversity loss in aquatic habitats worldwide. Inputs of sediment and nutrients act synergistically, leading to reductions in water quality, and alterations to deposition and flow in adjacent freshwater environments (Dudgeon et al., 2006). In Europe and North America, smothering of fish nests or “redds” can also affect the recruitment of commercially important anadromous fish such as salmon (Heaney, Foy, Kennedy, Crozier, & O'Connor, 2001).

Anthropogenically mobilized nitrogen and phosphorous in aquatic environments make their way downstream to coastal waters and are a substantial source of inshore nutrient enrichment (Howarth & Paerl, 2008). Marine habitats can become eutrophic as aquatic plants flourish from nutrient enrichment and subsequently die, depleting dissolved oxygen concentrations in bottom waters (Rabalais, 2002). Low oxygen availability (hypoxia) effectively compresses suitable habitat for foraging and reproduction in marine species, increasing local mortality (Breitburg, 2002). This may be exacerbated in coastal systems that naturally experience significant stratification, and where subsequently, oxygenated and oxygen-deficient water bodies are not able to mix, isolating benthic organisms in hypoxic environments (Diaz & Rosenberg, 2008). Nutrient-driven hypoxia that persists can produce large areas devoid of marine life known as “dead zones,” significantly reducing fisheries catch (Diaz & Rosenberg, 1995; Renaud, 1986). Over 400 dead zones exist in coastal areas worldwide, many of which are in major fishing grounds such as the Baltic Sea, East China Sea, and the Gulf of Mexico (Diaz & Rosenberg, 2008). As fish and invertebrates die and decay, they not only cause

further draw down of oxygen (creating positive feedback conditions), but huge biomass potential is lost from fisheries; estimates place this loss as high as 734,000 T C year⁻¹ over an area of 245 000 km² (Diaz & Rosenberg, 2008).

Diffusion of herbicides from land into coastal aquatic environments are of additional concern given their inhibiting effect on photosynthetic productivity—a threat to phytoplankton, mangroves, seagrasses, sponge, and coral symbionts (Kennedy et al., 2012). Herbicides used in sugarcane plantations in northeast Australian river catchments have been linked to widespread coastal mangrove die-back, and so the degradation of fish nursery habitat (Duke, Bell, Pederson, Roelfsema, & Nash, 2005). Reductions in coral or coralline algae growth rates from chronic exposure to sub-lethal herbicide concentrations also present an additive stressor affecting marine ecosystem function and services (Lewis et al., 2012).

While the flow of subsidies typically moves from land to sea, interactions are not always unidirectional. For instance, anadromous fish are important conduits of sea to land connectivity. Foraging in the ocean and dying in freshwater breeding grounds, they are important vessels of nutrient transfer between marine and terrestrial ecosystems (Gende, Edwards, Willson, & Wipfli, 2002). Fishing operations harvesting fish before they return inland may alter the flow of nutrients to the terrestrial ecosystems that support food production (Álvarez-Romero et al., 2011).

Management challenges on the Great Barrier Reef exemplify the consequences of ignoring ecosystem connectivity between land and sea. Despite the reef-zoning plan introduced in 2004, coral reef quality has continued to decline in central and southern reef regions in recent years (GBRMPA, 2014). A major contributor to this decline is poor water quality caused by dissolved inorganic nutrient run-off from river catchments outside of the Great Barrier Reef Marine Park (GBRMPA, 2014). Agricultural fertilisers, largely derived from intensive sugarcane production and horticulture in the Great Barrier Reef catchment are by far the largest nutrient source (GBRMPA, 2014; Waterhouse, Brodie, Lewis, & Audas, 2015).

Nutrient enrichment is also a hypothesis for a potential cause of increased larval survival of the Crown of Thorns Starfish (*Acanthaster planci*) (Wooldridge & Brodie, 2015). This large corallivorous starfish was responsible for over 40% of coral reef loss on the Great Barrier Reef between 1985 and 2012 (De'ath, Fabricius, Sweatman, & Puotinen, 2012). These downward trends in coral reef cover and habitat complexity, parallel steady decreases in catch per unit effort in both recreational and commercial reef fisheries (GBRMPA, 2014). Notwithstanding continued investment into improved land management practices by governments, regional management bodies, and landowners, land-based run-off still presents one of the greatest threats to the Great Barrier Reef (GBRMPA, 2014).

As food demands grow, the influence of agricultural run-off to freshwater and marine environments across the globe is of great concern. Fertilizer consumption continues to rise in the majority of countries to support crop production (Figure 2) and this trend is likely to persist. Cereal production alone will need to increase by one billion tonnes (from an early 2000s baseline) to meet 2050 food

demands (Alexandratos & Bruinsma, 2012). At present, animal feeds consume over 30% of crops grown and with a shift away from grazing to feed-dependent livestock systems, total fertiliser demand drawn from meat products is set to rise (Alexandratos & Bruinsma, 2012). Moreover, supplying greater demand for livestock products will directly contribute to increases in nutrient loading on land from manure. Global nitrogen and phosphorous wastes generated by livestock effluent already exceed that of fertiliser use (Bouwman et al., 2013). Thus, trends in human diets will be a major determinant of land-sea nutrient flow into the future. Consumption of animal-based protein is inherently inefficient in the transfer of nutrients from fertilizers to humans. Continued global trends towards current western diet portfolios will exacerbate regional surpluses of nitrogen and phosphorous in agricultural soils (Bouwman et al., 2013). Replacement of beef with poultry and pork and more plant-based diets, however, may prove effective in reducing these surpluses and the costs of terrestrial production for aquatic systems (Bouwman et al., 2013; Galloway et al., 2010).

In low-latitude countries, vulnerability to coastal enrichment is compounded, not just by pollution exposure, but the susceptibility of nitrogen-deficient tropical waters to eutrophication, and the high human dependence on fisheries for food security (Beman, Arrigo, & Matson, 2005). The implications of cross-system connectivity also extend beyond coastal waters and into management considerations for offshore marine areas. There is evidence to suggest that closure of open ocean areas (outside of exclusive economic zones) could result in greater fisheries yields (White & Costello, 2014) or at least reduced inequalities in fisheries distribution at a global level (Sumaila et al., 2015). This is, however, contingent on coastal waters remaining productive in the face of greater agricultural run-off potential. Thus, fisheries governance needs to consider terrestrial influences

on marine production and vice versa. While this is beginning to be recognised in Integrated Land-Sea Management plans that cover catchment to coastal ecosystems, examples of successful implementation are rare (Reuter, Juhn, & Grantham, 2016).

3 | FEED INTERDEPENDENCIES

Urbanisation and increased affluence are shifting human diets to greater proportion of animal-based protein. In 2009, the 15 wealthiest nations consumed 750% more ruminant, seafood, poultry, and pork meat per capita than the poorest 24 nations (Tilman & Clark, 2014). With growing demand for both terrestrial livestock and cultured aquatic organisms, the supply of feed must also keep pace (Boland et al., 2013; Tacon & Metian, 2015). Sourcing feed for livestock and fish production also increases inter-dependencies among food systems on land and sea (Blanchard et al., 2017; Troell et al., 2014).

Historically, both agriculture and aquaculture have depended on fishmeal and fish oil as important constituents of animal feeds. Fishmeal and oil are primarily sourced from small pelagic, or "forage" fish, caught and processed for non-food purposes (Fr  on et al., 2014; Tacon & Metian, 2009) and are a valuable source of high grade protein and long-chain, polyunsaturated fatty acids for domesticated animals (Stoner, Allee, Nelssen, Johnston, & Goodband, 1990). Nonetheless, dependence on fishmeal and oil inputs for animal feed has come under question as meat and fish production grows to meet consumer demand. Large-scale harvesting of small pelagic fish is implicated in the decline of several higher trophic level fish stocks, disrupting energy flow in marine food webs by removing key prey species for a range of organisms (Naylor et al., 2000). It has also

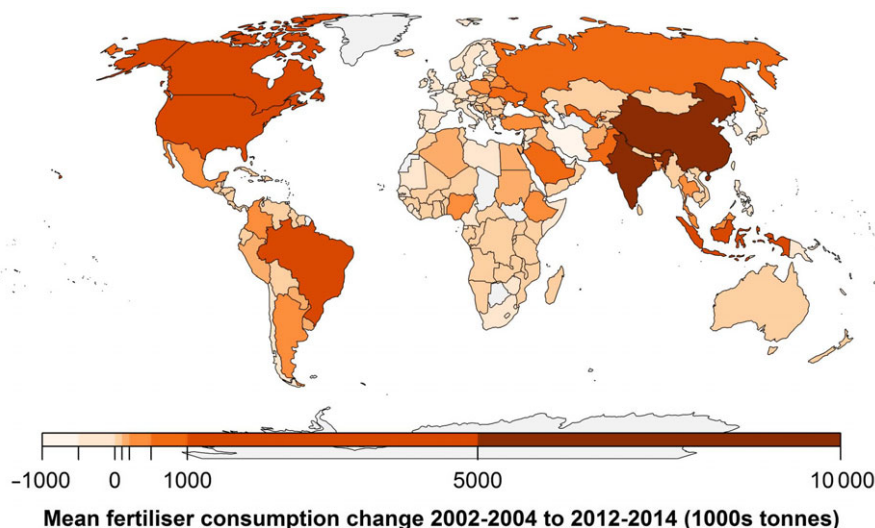


FIGURE 2 Global 10-year mean change in synthetic fertilizer consumption. Mean change in consumption calculated from differences in average nitrogen and phosphorus fertiliser consumption between 2002–2004 and 2012–2014 (scale in 1000s of tonnes). Total annual consumption equals domestic production plus imports minus exports. Grey shading represents countries with incomplete or no data for fertilizer consumption from 2002 to 2014. Data sourced from the Food and Agriculture Organization (FAO) of the United Nations (FAO, 2017a)

sparked debate about the use of marine resources as animal feed rather than for human food (Allison, 2011; Tacon & Metian, 2009; Wijkstrom, 2009).

To improve sustainability, and in response to rising fishmeal prices (Tacon & Metian, 2008), aquaculture is increasingly replacing marine ingredients with terrestrial proteins and oils in feed (Troell et al., 2014). Indeed, aquaculture demand for fish products has not grown in 20 years despite the many fold increase in production (Tacon, Hasan, & Metian, 2011). This is due to an increase in aquaculture efficiency, but also because crop products (such as soybean and maize) and by-products of livestock production (meat and bone meal) are increasingly used as fishmeal substitutes (Watanabe, 2002). Despite the nutritional challenges of increasing vegetable products in fish diets (Brinker & Reiter, 2011; Midtbo et al., 2015), technological progress has been rapid and some feed manufacturers now supply fishmeal-free aqua-feeds (Skretting, 2015; Skretting Australia, 2016). Fish-oil remains necessary within the feed of many carnivorous fish for now, but new research highlights the potential for substitution by marine algae (Sprague et al., 2015).

Aquaculture remains the largest consumer of fishmeal and oil (Tacon et al., 2011), but greater inclusion of crop-based ingredients in feeds means the terrestrial costs of aquatic production are also increasing. Feed crops and expansion of inland production is increasing aquaculture's reliance and pressure on freshwater resources (Gephart et al., 2017). Aquaculture's environmental impacts may now include agricultural run-off (Fry et al., 2016) and estimates placed global freshwater use between 31 and 39 km³ in 2008 (Pahlow, van Oel, Mekonnen, & Hoekstra, 2015). For the same year, Fry et al. estimate the land area required to grow the top five aquaculture feed crops (soybean, rapeseed, maize, groundnuts and wheat) was comparable to the size of Iceland (Fry et al., 2016).

Land is already a scarce commodity and becoming increasingly so across many nations of the world as croplands, pastures, biofuel feed stocks, urban areas, protected natural areas, and forestry plantations continue to expand (Lambin & Meyfroidt, 2011). While some activities are displaced into ocean areas (e.g. energy production), pressure on land use from food production, including aquaculture production will continue. There is great dependence on terrestrial livestock to supply increased meat demands globally (Naylor et al., 2005), but the growth of inland pond aquaculture—the largest source of farmed fish—may increase conflicts for space (Edwards, 2015; FAO, 2016). Aquaculture continues to outstrip the growth rate of other production sectors (Figure 3a), and while increasing competition for freshwater and land is pushing some forms of aquaculture further out in the marine space, this is not consistent everywhere (Troell et al., 2014). In areas where suitable coastal sites are unavailable or transition costs are too great, inland aquaculture is expanding into agricultural land. With competition for production space and feed crops, conflict between terrestrial and aquatic food systems has the potential to increase (Troell et al., 2014). This may be of particular concern in several Asian countries, which account for the majority of global inland aquaculture (Figure 3b), and where rapid population growth

and urbanisation create further constraints on land use (United Nations, 2014, 2015a).

Understanding the trade-offs between expansion/intensification of inland fish production and land used for agricultural purposes will be important as food demands rise (Edwards, 2015). Improving freshwater use efficiency in aquaculture will also need consideration as water scarcity increases (Edwards, 2015). Thus, there is a pressing need to establish how to best use current cultivated land for multiple pathways of food production. Greater conflict among sectors for land, water, and energy may disproportionately affect the food security of people in developing countries. The majority of non-cultivated land suitable for cropping is found in Latin America and Sub-Saharan Africa where a heavy burden of hunger and poverty already exists, and land and water-acquisition by foreign governments further redirects resources away from local markets into exported goods (Lambin & Meyfroidt, 2011; Rulli, Savioli, & D'Odorico, 2012).

Feed interdependencies continue to shift impacts of animal production in the opposite direction too. Pigs and poultry accounted for 20% and 5% of global fishmeal consumption respectively in 2010 (Shepherd & Jackson, 2013). While this proportion is significantly lower than fifty years ago, the pork industry's share of consumption has stayed relatively stable since the late 1980s (Tveterås & Tveterås, 2010). Lower vulnerability of the pork industry to fishmeal price increases is likely due to the disproportionately beneficial effect that even small fishmeal feed inclusions have on the growth rates of early-weaned piglets (Tveterås & Tveterås, 2010). Thus despite price increases, inclusion of fish inputs in specialty and starter feeds for terrestrial livestock are likely to persist into the future (Kristofersson & Anderson, 2006).

Maintaining and increasing crop production for feed and food is entirely dependent on access to phosphorous for fertilizer production (Neset & Cordell, 2012). Traditionally, manure, bone meal, and even human excreta were used to supply soils with phosphorous (Cordell, Drangert, & White, 2009). During the 19th century, significant deposits of seabird guano were mined on Pacific Islands and started to replace local phosphorous sources (Cordell et al., 2009), providing some of the earliest land-sea interdependencies in food production. Although, it was the discovery of phosphate rock sources on land that transformed fertilizer industries. These highly concentrated rock-derived nutrients were key to substantially increasing yields during the Green Revolution (Cordell et al., 2009).

Mineral phosphate sources are, however, a finite resource, with phosphate production expected to reach its peak at some point this century (Neset & Cordell, 2012). Now there is potential for the impacts of phosphate mining to spill over into the marine environment. Growing food demands require greater fertilizer supply, and phosphate deposits in margin sediments are currently being targeted for exploration off Namibia, New Zealand, and Mexico (Mengerink et al., 2014). The impacts of these dredging operations to benthic environments and fisheries are of great concern and uncertainty (Mengerink et al., 2014), and provide another example of how production demands in one sector may produce trade-offs in another.

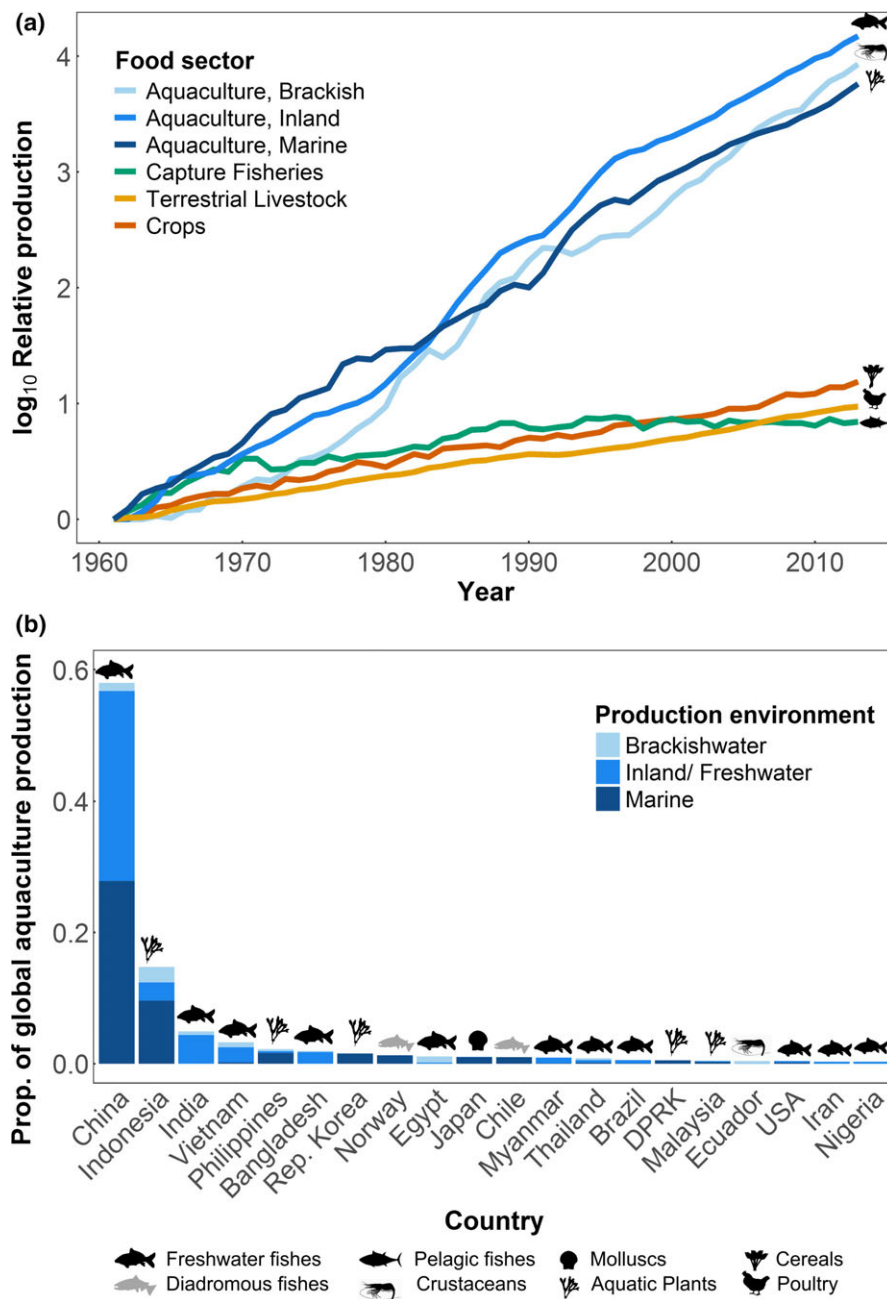


FIGURE 3 Cross-sector and spatial comparisons of global aquaculture growth and production. (a) Log-relative change in total aquaculture (inland, brackish and marine), terrestrial livestock, crop, and capture fisheries production from 1961 to 2013. Image symbols represent functional groups responsible for greatest absolute change (tonnes) within sector over time-period. (b) Proportion of global aquaculture production from top 20 producing nations (>95% of global production by weight) by culture environment in 2015. Image symbols represent largest functional group contributions to domestic production (tonnage) in 2015. Aggregate livestock, crop, and aquaculture commodity data sourced from the FAO (FAO, 2017a, 2017b) and capture fisheries data taken from Watson (2017)

Interdependencies among sectors do not exist or act in isolation, but also interact with the natural ecosystem connectivity mentioned in the previous section. In an ever-globalizing world, demands for animal feed now drive ecosystem change in areas distantly removed from animal production (Liu et al., 2013; Österblom, Crona, Folke, Nyström, & Troell, 2016). Production pollution, trade, processing, use, and the subsequent waste of feed products redistributes the flow of energy, nutrients, and organisms between aquatic and terrestrial ecosystems at macroecological scales (Figure 4).

Ultimately, sustainable food system development needs to consider inefficiencies associated with feeding a growing global population with greater proportions of animal-based protein. For example, Foley et al. (2011) calculate that an extra one billion tonnes of crop-based human food could be supplied by redirecting total

production of 16 major crops away from animal feed. Merino et al. (2012) estimated that aquaculture's high dependence on forage fish for feed could limit the capacity of aquatic production systems (cultured and wild caught) to meet seafood demands projected by 2050. Continued growth in the aquaculture sector will require either a greater market share in fishmeal and oil consumption or even further movement away from marine feeds to prevent ecological collapse in marine systems (Merino et al., 2012). But as aquaculture transitions to more crop-based feeds, food production pressures on land grow, increasing inter-sectoral conflict for resources, or further threatening terrestrial ecosystems through the expansion of agriculture (Foley et al., 2011; Mayaux et al., 2005; Newbold et al., 2015). Furthermore, relative contributions from pigs and poultry to total livestock production are increasing (Davis et al.,

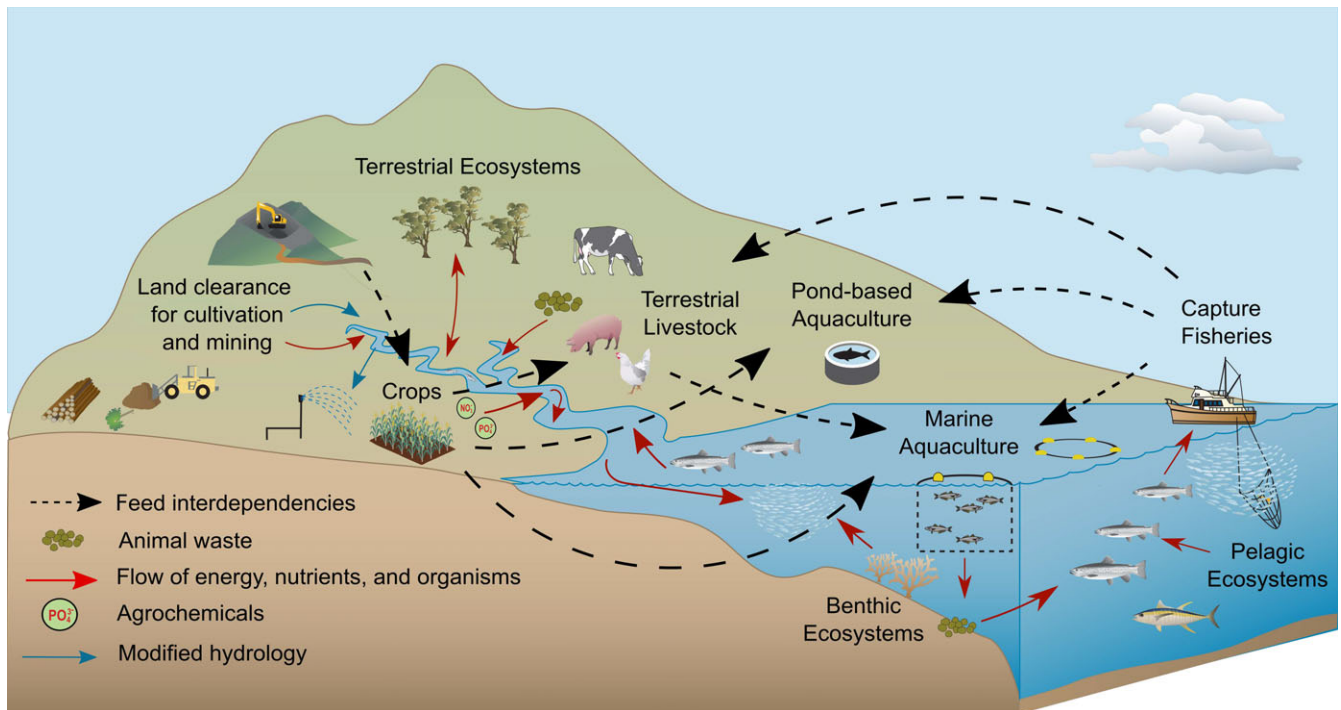


FIGURE 4 Feed interdependencies redistribute land-sea nutrient flows over large spatial scales. Run-off from land-clearance and agricultural nutrient waste influences the productivity of coastal waters globally, while fisheries may disrupt the flow of nutrients to terrestrial ecosystems. The trade, use, and waste of livestock and aquaculture feeds redistribute nutrients between land and sea, often over vast distances. Intensified use of feed products then contributes to aquatic and terrestrial nutrient surpluses, interacting with natural land-sea connectivity

2015). Whether these shifts pose a threat to marine systems through demands for fishmeal will likely depend on the meat industry's flexibility to switch feed ingredients under changing environmental and market conditions.

Advances in feed technology could play an important role in increasing the sustainability of future food production. Both insects and algae show potential as a source of protein and fatty acids for livestock as at least partial replacement for fishmeal and oil (Angell, Angell, de Nys, & Paul, 2016; van Huis, 2013). Both can be produced intensively within warehouses, fed by organic side streams, reducing land and water footprints of production (Sanchez-Muros, Barroso, & Manzano-Agugliaro, 2014). Seaweed products have also demonstrated their potential as a replacement for conventional crop fertilizers (Cole, Roberts, Garside, de Nys, & Paul, 2016). To what extent these novel products can substitute the aquatic and terrestrial resources currently used remains unclear, as does any unintended consequences of their use, but with current trends in diets it seems likely cross-sector feed interdependencies will persist in one form or another into the future.

4 | LIVELIHOOD INTERACTIONS

Resource partitioning of human livelihoods also link terrestrial, freshwater, and marine food systems across the globe. Mixed-farming methods, common throughout Asia, simultaneously integrate fish

production into agricultural systems. Waste from one sub-system of fish, cattle, or crop production is used as a nutrient or feed input for another (Ahmed, Ward, & Saint, 2014); reducing the need for off-farm labour, synthetic fertilizers and feed, improving household and resource efficiency (Begum, Islam, Khan, Islam, & Tapu, 2015; Blythe, 2013; Prein, 2002).

Livelihood diversification between terrestrial and aquatic systems may also compensate for seasonal changes to resource availability (Cinner et al., 2012). Supplementing terrestrial farming with aquatic production (and vice versa) at different times of year is a coping strategy documented across Asia, Africa, the Pacific Islands, and the Caribbean (Allison & Ellis, 2001; Fisher et al., 2017). For economies dependent on African inland fisheries for example, people fish lakes and waterways when they are in flood, then cultivate land exposed by receding floodwaters in the dry season (Sarch, 1996). In Indonesia, switches between rice or tree-crop farming and fishing are common in response to fish availability (Allison & Ellis, 2001). Alternating activities between sectors in response to fluctuating resources, improves the stability of local food availability throughout the year. Income gained from one sector is invested back into another, protecting against social-ecological shocks (Allison & Horemans, 2006; Cinner et al., 2012; Sarch, 1996) but also linking aquatic and terrestrial sectors through their own productivity. The prevalence of such inter-sectoral dependence in human livelihoods is widespread. Recent analysis of demographic and household data from three continents reveals how coastal fisheries-dependent communities more

commonly co-depend on terrestrial production than not (Fisher et al., 2017).

Human adaptation strategies that produce land-sea switches can, however, also serve as a compounding stressor on recipient sectors—shifting the pressures of human food provision to one system when resources in another fail. During times of poor coastal fish harvests, the coastal communities most affected may seek alternative livelihoods in bushmeat hunting or agriculture for income generation and sustenance (Brashares et al., 2004). Unsustainable wildlife harvesting may increase as deforestation for agricultural and timber production open up forests to hunters and the bushmeat trade (Houghton, 2012). The reverse trend has occurred where poorly planned water development programs, resource-based corruption, or drought on land displaces nomadic pastoralists and farmers to the coastline (Collins, 2016). Shifts from terrestrial systems that lead to unregulated increases in fishing capacity can exacerbate trends of declining catches, overexploiting marine resources in an effort to maintain income (Collins, 2016; Pauly, 1994). Erosion of resources and livelihood options like this are also a driver for maritime piracy, and a connection to wider clan-based crime networks (United Nations Security Council, 2016). Understanding how changes to food production in different sectors will displace human resource use across ecosystem boundaries, will become increasingly important in a world where global change influences ecosystem services and food resources across multiple sectors on land and sea.

Where food intensification pathways fail to consider cross-system impacts on other sectors, subsequent shifts between agriculture and seafood production may be a source of significant social-ecological conflict and reduced food security. The rapid expansion of intensive shrimp aquaculture in Southeast Asia provides a prominent example. Producing luxury goods destined for growing developed world markets, shrimp farming represents considerable export potential for developing countries and is now the second largest aquaculture industry by value (FAO, 2016). The profitability of shrimp production has led to rice farmers across Vietnam, Thailand, India and Bangladesh converting paddy fields into shrimp ponds to boost

household income (Bhat & Bhatta, 2004; Dung, Hoanh, Page, Bousquet, & Gajasen, 2009; Gowing, Tuong, Hoanh, & Khiem, 2006; Ito, 2002). But the dramatic transition in resource use has also led to widespread conflicts among modern and traditional food producers in coastal Asia.

As aquaculture has expanded, mangrove areas are cleared and ponds extended landward (Figure 5a,b). Intrusion of salt water from shrimp ponds into adjoining agricultural land has salinized soil and groundwater in many areas, resulting in reduced grazing land and lowered crop productivity (Paul & Roskaft, 2013; Paul & Vogl, 2011). Clearance of mangrove forests for pond structures negatively influences local fisheries by reducing mangrove-associated stocks and blocking fishers access to the coast (Ahmed & Glaser, 2016; Primavera, 2006). Furthermore, mangrove deforestation places coastal communities at greater risk of flooding from storm events or sea-level rise (Ahmed & Glaser, 2016) and reduces the availability of vegetative materials (such as fruits or herbs) originally farmed or collected from the mangrove forests themselves (Jusoff & Bin Hj Taha, 2008).

While more affluent individuals and families may be able to transition into shrimp cultivation, those rice farmers or fishers with lower household capital have few alternatives for income generation (Paul & Vogl, 2011). As a result, many turn to felling mangrove vegetation to sell as firewood, worsening biodiversity loss, inter-sectoral conflict and the risk of coastal flooding and storm damage (Paul & Vogl, 2011). Forceful displacement of traditional landowners has been reported in many areas and the less labour-intensive aquaculture rarely provides sufficient positions for alternative income (Gowing et al., 2006; Paul & Vogl, 2011). Consequently, the surplus rural workforce are increasingly marginalized, becoming refugees of aquaculture expansion, and may be forced to migrate to cities, compounding the issue of urban poverty and food insecurity (Gowing et al., 2006).

Best management practices continue to improve resource-efficiency of shrimp farming (Paul & Vogl, 2011) but the social-ecological complications surrounding these intensive systems provide a stark example of how meeting global food demands without

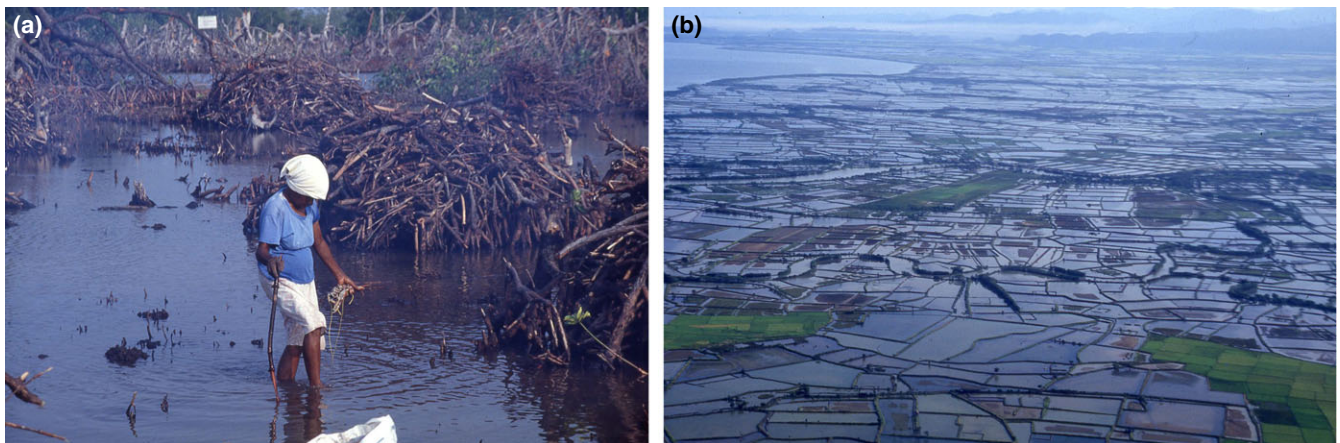


FIGURE 5 Cross-sector livelihood conflicts. (a) Local fisher foraging after clearance of a mangrove forest for shrimp aquaculture development in Irian Jaya, Indonesia. (b) Expansive shrimp aquaculture located in former mangrove wetlands near Ujang Pandang, Sulawesi, Indonesia

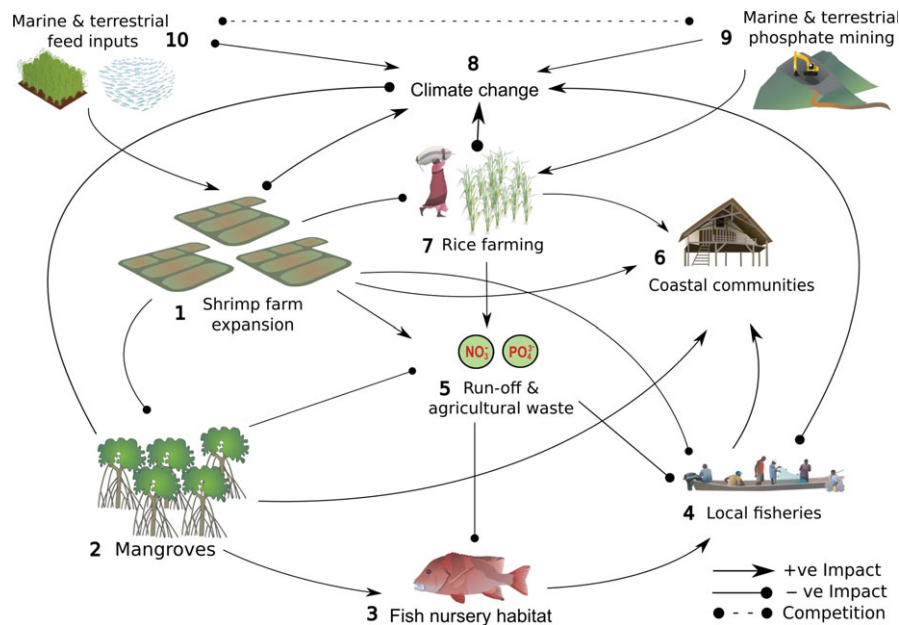


FIGURE 6 Intensive Shrimp Farming as an example of complex social-ecological, land–sea interactions. Bracket numbers and arrows describe figure interaction pathways resulting from the expansion of shrimp farming (1). Livelihood benefits for adaptable households (1→6). Negative impacts on fisheries livelihoods from mangrove clearance (1→2→3→4→6 or 1→5→3→4→6 or 1→2→5→3→4→6), pollution (1→5→4→6), and reduced beach access (1→4→6). Negative impacts on rice farmer livelihoods from degraded soil and coercive displacement (1→7→6). Aquaculture, fisheries, and farming are impacted by climate change (8→1, 8→4, 8→7) but also emit greenhouse gases (1→8, 4→8, 7→8). Removal of mangrove forests reduces carbon storage (1→2→8) and increases risk of coastal flooding (1→2→6). Agriculture and aquaculture also rely on fertiliser (9→7) and feed inputs (10→1) which both contribute to climate change (9→8, 10→8) and compete for land, water and energy at macroecological scales (9→10)

considering cross-sector trade-offs can fundamentally undermine food security at local levels. Changes to, or diversification of human livelihoods discussed above, alter patterns of terrestrial and aquatic resource use through the temporal or spatial partitioning of food production activities. Development of food systems from single sector perspectives ignores cumulative and interactive ecosystem impacts acting across sectors and overlooks the effect of shifts in resource use onto other ecosystems arising from livelihood adaptation. Critically, this interplay among sectors is occurring against a backdrop of environmental variation and change. We use the social-ecological feedbacks produced from intensive shrimp farming as an example to illustrate the synergies between ecosystem connectivity, feed dependencies, livelihood interactions, and climate feedback (Figure 6).

5 | CLIMATE FEEDBACK

Terrestrial and aquatic food sectors significantly contribute to greenhouse gas emissions, and are in turn impacted by climate change; providing further, albeit, indirect links between land and sea.

5.1 | Emissions from food production

Food production contributes to carbon dioxide (CO₂) emissions through the use of fuel-driven machinery and the processes of packaging, transportation and spoilage along the supply chain (Sonesson,

Davis, & Ziegler, 2010). Carbon dioxide is the primary emission from capture fisheries which are heavily dependent on fossil fuel for harvesting wild fish (Avadí & Fréon, 2013; Tyedmers, Watson, & Pauly, 2005). But emissions differ considerably between size of vessels, gear types, and on board traditions (Basurko, Gabiña, & Uriondo, 2013).

Primary agriculture and aquaculture greenhouse gases emissions originate from their production cycles and these vary greatly in quantity and form. Terrestrial agriculture acts as both a sink and a source of atmospheric CO₂, but substantial emissions of methane and nitrous oxide are also produced, which hold greater global warming potential (Smith et al., 2014). Agriculture is the greatest contributor to non-CO₂ emissions globally (Smith et al., 2014); methane produced by cattle rumination is the single greatest source (Sonesson et al., 2010). Although, novel feed ingredients, such as seaweed, show promise for reducing methane production (Maia, Fonseca, Oliveira, Mendonça, & Cabrita, 2016). Outside of the production cycle, land clearing is also responsible for huge releases of CO₂ and contributes to warming via alterations to the albedo of the Earth's surface (Myhre et al., 2013; Smith et al., 2014).

Only recently has attention focussed on emissions from aquaculture production. Dissolved ammonia and ammonium are generated in aquaculture systems from faeces and waste feed (Hu, Lee, Chandran, Kim, & Khanal, 2012). These are converted to nitrate and then into nitrogen and nitrous oxides by nitrifying and denitrifying bacteria respectively (Hu et al., 2012). The quantity of emissions produced by a given operation depends on methods of nitrogenous waste

disposal, feeding rate, water pH, salinity and oxygenation (Hu et al., 2012), but conservative estimates suggest aquaculture currently produces ~4% of agricultural emissions (Williams & Crutzen, 2010). With the current growth rate of aquaculture, this could rise to 20% by 2030, particularly as a switch to plant-based feeds may increase nitrous oxide emissions from the crop-growing phase (Williams & Crutzen, 2010).

5.2 | Climate change consequences for terrestrial and aquatic food systems

Climate change influences food systems on both land and sea. On land, changes to temperature, precipitation and CO₂ concentrations influence crop growth rates, the duration of growing seasons, water availability, soil moisture, viability of grazing pastures, and the frequency of storm events (Calzadilla et al., 2013). While in the oceans, warming and acidification drive changes to marine species survival, distribution, and reproduction by influencing a number of biotic and abiotic factors. Warmer, more acidic water alters patterns in salinity, circulation, stratification, storm event frequency, and ecosystem structure; and influences metabolic function and behaviour of many vertebrates and invertebrates (Doney, Fabry, Feely, & Kleypas, 2009; Laffoley & Baxter, 2016; Messmer et al., 2016; Rhein et al., 2013; Rummer & Munday, 2017).

Global agricultural production is expected to decrease by 2%–3% over the next 30 years due to climate change, leading to reductions in human welfare of over USD \$300 billion (Calzadilla et al., 2013). Impacts will vary spatially. Warmer temperatures, greater precipitation, and carbon fertilization may benefit crop yields in higher latitudes, through shorter frost periods and increased water availability (Rosenzweig et al., 2014). In contrast, even moderate temperature increases in low latitudes are expected to decrease crop yields by lowering water availability for rain-fed systems and reducing soil moisture (Calzadilla et al., 2013; Rosenzweig et al., 2014).

The effects of climate change on fisheries will also differ geographically. As a response to warming, marine species continue to track preferred temperature conditions, migrating offshore and polewards to cooler waters (Allison & Bassett, 2015; Pecl et al., 2014). Species shifts such as these are expected to redistribute global catch potentials, decreasing the productivity of tropical fisheries in particular, and increasing catch in temperate regions (Barange et al., 2014; Cheung, Watson, & Pauly, 2013; Pecl et al., 2014). Although, the catch of fleets from high latitude countries operating in foreign tropical waters are also likely to sustain losses (Lam, Cheung, Reygondeau, & Sumaila, 2016). Latitudinal shifts are of great concern for inland fisheries too, where redistributions within freshwater systems may cross national borders (Ficke, Myrick, & Hansen, 2007). The inability for some species to track thermal gradients in east-west orientated systems may also lead to changes in fisheries structure as more thermal tolerant species prevail (Ficke et al., 2007), with unknown consequences for local economy, ecology, and human well-being.

Despite latitudinal trends, patterns of climate change impacts vary across similar latitudes on land or in the ocean; instead

particular hotspots are expected. Tropical South America, South Asia and some areas of Africa (such as the Ethiopian highlands) are all expected to experience reductions in agricultural productivity over the coming decades (Piontek et al., 2014). Further, these declines will likely be experienced in combination with other cumulative stressors such as water scarcity and ecosystem degradation (Piontek et al., 2014). Twenty-four hotspots of rapidly warming areas in the global ocean have also been identified, and the majority are found in tropical regions (Hobday & Pecl, 2014). Of particular concern are areas projected to experience simultaneous reductions in fisheries and agricultural productivity under climate change. While some European countries (e.g. Norway and the UK) may experience such double jeopardies, simultaneous land-sea impacts are likely to disproportionately affect people in developing nations of low adaptive capacity, high population growth, and heavy hunger burdens (Blanchard et al., 2017).

Aquaculture may be the exception to the trend of a widening production gap between high and low latitude countries. The temperature changes expected in the tropics are within the optimal ranges for most cultured species and warmer waters may increase feed utilization efficiency and growth rates in marine, freshwater and brackish production (De Silva & Soto, 2009). In contrast, aquaculture in higher latitudes is more vulnerable to warming. For example, the huge salmon industry relies on a narrow temperature band for optimum fish growth (Bell et al., 2016). Relocation of salmon farms is already happening in response in southern Tasmania, Australia. Potential resilience of tropical aquaculture could provide a solution for countries experiencing the greatest reduction in fisheries and agriculture, although at present, only a handful of countries account for the majority of aquaculture production (Figure 3b). Expanding aquaculture in countries that need to counteract decreases in other food sectors will require coherent policy developments that encapsulate a wide range of interacting economic, social, and environmental factors (Beveridge, Phillips, Dugan, & Brummet, 2010).

Beyond food availability, climate change will also impact food access, stability and utilization into the future (Wheeler & von Braun, 2013). Variability of crop production can influence food prices and thus purchasing access or income from food production (Nelson et al., 2014). In fisheries, biogeographical distribution shifts can affect operational costs, economic rents and fish prices (Sumaila, Cheung, Lam, Pauly, & Herrick, 2011). Changes to production also influence international trade. Russia, South Asia and the Middle East are likely to see reductions in welfare arising from lower competitiveness of agricultural product. In contrast, sub-Saharan Africa, China and northern South America may see their relative trade position improve (Calzadilla et al., 2013). These effects may also be occurring against a background of changing disease pressure on agriculture and aquaculture systems (Bell et al., 2016; Wheeler & von Braun, 2013) and greater instability of production brought about by increased climate variability (Wheeler & von Braun, 2013). Food security in the most threatened regions is further threatened as people become displaced or impoverished by more frequent extreme weather events, sea-level rise, water scarcity (Gemenne, 2011).

Finally, climate change is also likely to influence the land–sea interactions discussed here. Changes to precipitation regimes and extreme weather events expected will alter hydrology, dictate the need for fertiliser and pesticide applications, and determine to what extent agricultural nutrients can influence aquatic environments. Climate-induced changes to the availability, accessibility, stability, and safety of crop and livestock resources, including any influence on trade, will affect both the quantity and quality of both marine and terrestrially sourced feed products. Spatial shifts in marine or terrestrial production will also have implications for the livelihoods of people in the recipient and vacated regions with, as yet, unknown effects.

6 | BRIDGING THE LAND-SEA DIVIDE: PROGRESS, CHALLENGES AND SOLUTIONS

We have shown that the nexus of ecosystems, feed production, human livelihoods and climate fundamentally link food systems on land and sea (Figure 7). Yet integration of aquatic and terrestrial components in food security research and policy is lacking. Accounting for, and where possible, addressing land–sea interactions will provide a crucial mechanism for preventing unintended outcomes from food system development.

Support for cross-sector research is growing, and modelling that integrates food production with social-ecological drivers of change presents a powerful approach of accounting for land–sea interactions described here. Work emerging from the Inter-Sectoral Impact

Model Inter-comparison Project (ISIMIP) quantifies impacts and trade-offs among agriculture, fisheries, water, energy, agro-economics, infrastructure, forestry, ecosystems, and health sectors under climate change (www.isimip.org). The GLOBIOM model developed by the International Institute for Applied Systems Analysis (IIASA), analyses resource pressure among agricultural, bioenergy, and forestry sectors. Recent development of the “Madingley Model” aims to integrate links between marine and terrestrial ecosystems in order to project human impacts at a global scale (Harfoot et al., 2014). Nonetheless, more integrative and empirical work is needed for food security research. For example, no food production model holistically incorporates both marine and terrestrial components.

Single-sector approaches to research mean that combined solutions from aquatic and terrestrial production are vastly underrepresented in major food security policies and initiatives (Fisher et al., 2017). Land–sea connectivity in the food system presents a number of challenges regarding where to set boundaries of governance and how to engage actors at local scales to promote cross-system resilience (Pittman & Armitage, 2016). Matching the scale of the food security problem to the local and social contexts where solutions are enacted is a significant challenge for policy-makers. Overcoming the inherently complex and social-ecological nature of these problems, requires greater institutional support for inter- and transdisciplinary science that facilitates the exchange of diverse knowledge types among researchers, policy makers, and stakeholders (Pittman & Armitage, 2016).

Specialised taskforces on food security such as the “UK-US Taskforce on Extreme Weather and Global Food System Resilience”

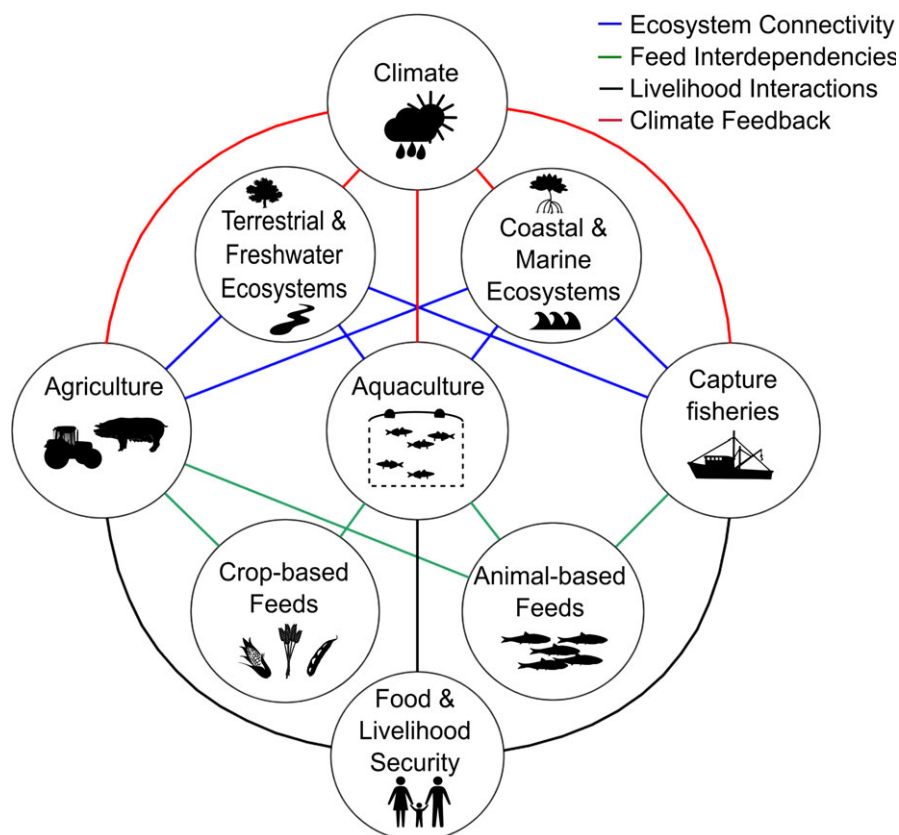


FIGURE 7 The nexus of land–sea interactions among food systems. Ecosystem connectivity, feed production, human livelihoods, and climate fundamentally link terrestrial and aquatic food production systems

(www.foodsecurity.ac.uk) and the United Nations “High-level Panel of Experts on Food Security and Nutrition” (www.fao.org/cfs/cfs-hlpe) represent an ideal opportunity for tackling these cross-sector challenges. Comprising academic, industry and policy professionals, these panels are in a unique position to encourage discussions on single sector targets and cross-sector trade-offs. For example, participatory inter-sectoral workshops in Colombia have proved effective in illuminating cross-sector conflicts among single sector development targets, facilitating integrated development planning and multisector collaboration (Weitz, Nilsson, & Davis, 2014). Bridging science and policy, these taskforces could implement similar approaches, and the High Level Panel on Food Security has already outlined that greater integration of aquatic and agricultural production is needed in future food security policies (HLPE, 2014).

Directly addressing counter-productive land-sea trade-offs in the food system will require significant improvements in food production efficiency. Integrating livestock waste into crop production, greater adoption of integrated pest management strategies and shifts towards agroforestry may improve on farm biodiversity while reducing impacts on aquatic ecosystems (Godfray et al., 2010). Precision technologies can be used to optimise timings and locations of chemical/nutrient inputs to prevent surpluses building in soils (Day, Audsley, & Frost, 2008). Increasing crop productivity in low yielding areas may also reduce the need to expand cultivated land area with rising feed demands, although this will vary spatially. In some areas, returning degraded agricultural land to food production may be less environmentally costly than improving yields for example (Godfray & Garnett, 2014). Diversifying food systems to integrate both aquatic and agricultural production can improve nutrient, land and freshwater use efficiency, but will also be key in increasing livelihood resilience to climate shocks in nations where food security remains a challenge (Blanchard et al., 2017). Furthermore, aquatic-terrestrial integration may provide a compromise in areas where inter-sectoral resource competition hinders food security, as with conflicts surrounding intensive shrimp farming (Paul & Roskaft, 2013).

Human consumption patterns in high-income countries must also change. Diets that reduce animal-based protein intake, optimise consumption within the bounds of human health and nutrition, reduce fertiliser and feed demands, and can lower food-related emissions (Davis et al., 2016; Foley et al., 2011; Gephart et al., 2016; Tilman & Clark, 2014). Domestic and commercial waste in the supply chain remains a huge source of inefficiency in the food system and may worsen with more resource-intensive diets. Global wastage of meat products alone represent crop losses sufficient to feed over 200 million people (Davis & D’Odorico, 2015).

Encouraging change will be difficult. Shifting diets at the population level may depend more on price and accessibility than environmental benefits (Popkin, Adair, & Ng, 2012). Simply redirecting feed crops and fish to human consumption also overlooks more complex socio-economic considerations, such as widespread dependence on livestock for livelihoods (Godfray et al., 2010), or distribution costs which limit poorer, rural communities’ access to forage fish products (Wijkstrom, 2009). Nonetheless, addressing this challenge, along with

other inefficiencies in food production, will be crucial for meeting sustainability targets outlined for 2050.

7 | CONCLUSIONS

As we strive to feed a growing population with more resource-intensive diets over coming decades, cross-sector links and interdependencies may create trade-offs for food systems on land and sea. Terrestrial food production is increasing pressure on aquatic systems through agricultural run-off and rising feed demands for livestock. In contrast, aquaculture now competes for terrestrial resources for feed to keep pace with sector growth. Improving land, pest and waste management, changing consumer diets and integrating terrestrial and aquatic production on larger scales may be central to addressing the counter-productive links driven by inefficiencies in the food system. Food security policies also need to better account for diverse livelihoods that simultaneously rely on both land and sea. Single system approaches for tackling hunger may underestimate vulnerability to global change as it reaches across multiple sectors and ecosystems. Research on how to anticipate cross-sector trade-offs in food and sustainability planning will play a pivotal role in informing policy in years to come.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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