REVIEW

Conserving connectivity: Human influence on subsidy transfer and relevant restoration efforts

Emily V. Buckner , Daniel L. Hernández, Jameal F. Samhour

Received: 20 March 2017 / Revised: 14 July 2017 / Accepted: 27 October 2017 / Published online: 10 November 2017

Abstract Conservation efforts tend to focus on the direct impacts humans have on their surrounding environment; however there are also many ways in which people indirectly affect ecosystems. Recent research on ecological subsidies—the transfer of energy and nutrients from one ecosystem to another—has highlighted the importance of nutrient exchange for maintaining productivity and diversity at a landscape scale, while also pointing toward the fragility of ecotones and vulnerability of subsidies to human activities. We review the recent literature on landscape connectivity and ecosystem subsidies from aquatic systems to terrestrial systems. Based on this review, we propose a conceptual model of how human activities may alter or eliminate the flow of energy and nutrients between ecosystems by influencing the delivery of subsidies along the pathway of transfer. To demonstrate the utility of this conceptual model, we discuss it in the context of case studies of subsidies derived from salmon, marine mammals, sea turtles, sea birds, and shoreline debris. Subsidy restoration may require a different set of actions from simply reversing the pathway of degradation. We suggest that effective restoration and conservation efforts will require a multifaceted approach, targeting many steps along the subsidy transfer pathway, to address these issues.

Keywords Conservation · Ecotone · Ecological subsidies · Landscape connectivity

INTRODUCTION

Ecological subsidies of energy and nutrients across ecotones can be important to ecosystem functioning in recipient systems, but are vulnerable to disruption from human

activities (Schulz et al. 2015; Larsen et al. 2016). Ecosystem conservation research often primarily focuses on the direct impact of human activities on the immediate surrounding environment, examining the effects of activities such as deforestation, overharvesting, and pollution on the productivity, diversity, and function of the systems in which those activities occur. However, as our knowledge of ecosystem connectivity and coupled human-natural systems has increased, research has begun to examine how the impacts of human activities may have a larger reach, extending past the target system to influence neighboring non-target ecosystems (Baxter et al. 2004; Massol et al. 2011) via the transfer of ecological subsidies (Polis et al. 1997). Studies have pointed to activities like habitat modification, introduced species, and water pollution, which indirectly impact the biodiversity and function of surrounding ecosystems due to their interruption, enhancement, or elimination of the transfer of subsidies, as examples of how humans can influence the environment at many different points across a connected landscape (Schulz et al. 2015; Larsen et al. 2016).

The flow of energy and nutrients from highly productive donor systems to less productive recipient systems is an important ecological phenomenon that connects ecosystems (Polis and Hurd 1996; Polis et al. 1997; Cloern 2007). Subsidy transfer can take place across any ecotone where energy or nutrients are transported across the system boundary (Polis et al. 1997). Connectivity is regulated by ecosystem boundaries (synonymous here with ecotones and interfaces), which function as semi-permeable points of interaction between distinct ecosystems or habitats (Puth and Wilson 2001). Ecological subsidies can cross boundaries either due to passive or self-propelled mechanisms, such as in the case of algal wrack deposition on shorelines and salmon migrations from marine to freshwater

ecosystems (Polis et al. 1997). Alternatively, subsidies may require a biological vector, such as in the case of guano deposition by seabirds in terrestrial environments (Polis et al. 1997). Subsidies can provide a significant component of the energy and nutrient availability in an ecosystem (Anderson and Polis 1999).

In the last 20 years, there has been a marked development in research regarding ecosystem subsidies, with over a 20-fold increase of papers published per year between 1997 (when Polis et al. defined the term ‘ecological subsidy’) and 2017, including several comprehensive literature reviews and syntheses (Leroux and Loreau 2008; Hocking and Reimchen 2009; Muehlbauer et al. 2014; Richardson and Sato 2015; Soininen et al. 2015). However, in spite of this increase in knowledge, there have been few studies (only 13% of total papers published) that look at the challenges associated with the conservation and management of ecological subsidies (for exceptions, see Schulz et al. 2015; Larsen et al. 2016). The delivery of ecological subsidies is both directly and indirectly impacted by human activity, and the conservation of subsidies requires a recognition of the various ways in which humans affect their delivery to recipient systems. In this paper, we construct a conceptual model that describes where human activities have influence along the path of subsidy transfer and offer some generalizations regarding the conservation and restoration of ecological subsidies. We highlight a series of case studies that illustrate and support the conceptual model and suggest relevant conservation and restoration methods to address human disruption specific to them.

CONCEPTUAL MODEL FOR HUMAN IMPACTS ON ECOLOGICAL SUBSIDIES

We developed a conceptual model for considering the impacts of human activities on the transfer of ecological subsidies based on two primary factors. First, we recognized that human activities can directly or indirectly influence the quantity and quality of subsidies that are transferred between a resource’s system of origin (‘donor’ system) and its final destination (‘recipient’ system). Second, we establish whether this influence can occur before, during, or after the transfer. Below we explain in greater detail how each of these two factors manifest.

Existing literature points to both direct and indirect effects of human activities on the flow of subsidies, as well as top-down and bottom-up trophic mediated influences. Subsidy transfers that occur via passive and self-propelled mechanisms can be interrupted by direct, physical impediments, such as habitat modification (e.g., dams and roadways; Puth and Wilson 2001). Human activities can also

indirectly alter the flow of these subsidies, such as through global change (Larsen et al. 2016), or when species introductions reduce subsidy availability for native species (Knight et al. 2005; Epanchin et al. 2010). Similarly, subsidies that require transfer via a vector can be disrupted directly by human activity, such as by preventing the biological vector’s access to a subsidy (i.e., a decrease in the availability of the subsidy (Schindler et al. 2003)), or indirectly, such as by altering trophic dynamics that impact the abundance or behavior of the vector (Fukami et al. 2006). In general, human activities that result in a change to the abiotic environment or to trophic levels below the subsidy impact that subsidy via bottom-up cascading effects, while activities that are directly exploiting the subsidy or result in a change to the trophic level above the subsidy impact the subsidy via top-down cascading effects (Schulz et al. 2015).

Top-down- and bottom-up-mediated, and direct and indirect impacts of human activities on subsidy transfers can happen at any point along the transfer pathway and often can be characterized in broadly similar ways. However, the strategies associated with restoring the subsidy transfer are often implemented in different habitats and ecosystems under different management jurisdictions and with different social implications. Thus, we categorized these impacts into three types: (1) when human activity within the donor system leads to a decline in the subsidy’s availability, (2) when human activity along an ecosystem boundary blocks the transfer of the subsidy, and (3) when human activity within the recipient system leads to a decline in the subsidy’s vector (Fig. 1). This conceptual model allows for the classification of specific examples of ecological subsidies that are affected by different human activities. In turn, the classification can be used to evaluate the potential effectiveness of proposed conservation efforts to restore and/or replace those subsidies.

METHODS

We conducted a literature search in Web of Science for papers published on the topic of ecological subsidies from 1997 to 2017. For our topic search, we used the words *allochthonous subsid** OR *spatial subsid** AND *ecological NOT geo**. To find papers published on ecological subsidies and their conservation, we used the refined search word *manag**. We next selected three case studies that demonstrate different delivery pathways of subsidies from aquatic to terrestrial systems and the human impacts on each pathway. Although subsidies can be transported between or across terrestrial and aquatic ecosystems in both directions (Polis et al. 1997), we focus here on the flux from water to land. Conservation efforts thus far have

Fig. 1 Conceptual model highlighting the three different ways by which human activities may influence the quantity or quality of an ecological subsidy as it moves from its system of origin ('donor' system) to its destination ('recipient' system). (1) When human activity within the donor system leads to a decline in the subsidy's availability, (2) when human activity along an ecosystem boundary blocks the transfer of the subsidy, and (3) when human activity within the recipient system leads to a decline in the subsidy's facilitator. For each category, we have provided examples of human activities, whether those activities are top-down or bottom-up mediated, and the subsequent effects those activities may have on the subsidy in question

focused primarily on subsidies moving from the human-dominated terrestrial environment into water bodies. However, aquatic to terrestrial subsidies are particularly important for the functioning of the recipient ecosystem and can be severely disrupted due to human activity (Larsen et al. 2016). With the majority of the human population concentrated along coastlines and waterways (Vitousek et al. 1997), the ecotone connecting land and water is likely one of the most disturbed in the world.

We present several case studies (Pacific salmon, beach wrack, and seabirds, sea turtles, and marine mammals—summarized in Table 1) that illustrate how an aquatic-derived subsidy can impact a terrestrial ecosystem and be influenced by human activities. We chose these specific examples because they are some of the best-described ecological subsidies in the current literature and they have some of the most compelling conservation measures intended to mitigate human-induced disturbance that could be applied to the restoration and preservation of subsidy transferal and ecosystem connectivity.

CASE STUDIES

Salmon

The migration of Pacific salmon (*Oncorhynchus spp.*) is one of the most thoroughly studied examples of an aquatic to terrestrial subsidy, and evidence that human activities influence this transport is well supported in the literature. Salmon subsidize stream ecosystems by moving marine-derived energy and nutrients to inland riparian areas (Helfield and Naiman 2001; Christie et al. 2008; Holtgrieve and Schindler 2011). However, salmon require a biological vector (i.e., their consumers) to cross the riparian interface and effectively subsidize terrestrial ecosystems (Hilderbrand et al. 1999; Gende et al. 2002). The rich marine-derived nutrients provided by salmon carcasses can be traced from spawning streams to vegetation far inland and within non salmon-consuming animals, indicating the far-reaching effects of this subsidy (Hilderbrand et al. 1999; Christie et al. 2008). Thus, the decline in salmon

Table 1 Aquatic to terrestrial subsidy case studies, with identified transfer process/type, human impact type, possible conservation strategies and explicit conservation literature, and possible resulting social implications or challenges

Case study (subsidy)	Aquatic to terrestrial process	Transfer type (S = self-propelled; P = passive; V = biological vector)	Human impacts on donor system		Human impacts on transfer pathway		Human impacts on recipient system	
			Top-down mediated	Bottom-up mediated	Top-down mediated	Bottom-up mediated	Top-down mediated	Bottom-up mediated
Salmon	Salmon carcass distribution across riparian systems	S, V	Overharvesting	Hatchery fish competition	–	Hydroelectric dams and river barriers	Loss of predators and carcass transporters (eagles, bears, etc.)	Degradation of stream, riparian area, and surrounding ecosystem Hatchery fish competition
Beach Wrack	Detritus accumulation along shoreline	P	–	Introduced macro-algal competition	Beach grooming	Shoreline armoring	–	–
Seabirds, Sea Turtles, and Marine Mammals	Guano distribution and accumulation along island/coastline systems Beach nesting; excrement, turtles, and eggs all nutrient sources Onshore defecation and mortality	S, P, V	Direct exploitation or accidental mortality (vessel collision, entanglement, bycatch, sonar interference)	Commercial fishery competition	–	Light pollution deterrent, nesting habitat loss due to human development	Guano mining/removal, Nest exploitation	Introduced predators and vegetation disrupt shorebird nesting
Case Study (Subsidy)	Possible conservation/restoration strategies						Possible social implications/challenges	
	For donor system impacts		For transfer pathway impacts		For recipient system impacts			
Salmon	Regulate commercial and recreation salmon catch (Schindler et al. 2010)	Remove/restore dams (Stanley et al. 2003; Pess et al. 2008; East et al. 2015; Foley et al. 2017) Construct effective fish ladders (Martins da Silva et al. 2012)	Reconnect isolated high-quality fish habitat and add in-stream habitat enhancements (Roni et al. 2002) Restore spawning habitat (Roni et al. 2002; Thomas et al. 2015) Prioritize streams which support the highest spawning biomass and rates of nutrient transfer (suggested ≤ 2 km reach) (Hocking et al. 2009) Artificially fertilize riparian systems (Gende et al. 2002; Compton et al. 2006; Kohler et al. 2012) Protect and/or regulate exploitation of vector species (Service 1993)	Shifts in regulation/policy for commercial and recreational fisheries (Ruckelshaus et al. 2002; Schindler et al. 2010; Richerson and Holland 2017) Changes to individuals' livelihood/lifestyle (Schindler et al. 2010) Economic impacts (Cline et al. 2017)				
Beach Wrack	Monitor/eradicate introduced species (Bishop and Kelaher 2013a) Effective conservation and management of near-shore marine ecosystems (Liebowitz et al. 2016)	Armor removal and shoreline restoration (Toft et al. 2014; Gittman et al. 2016) Armor setbacks (Dethier et al. 2016) Regulate beach grooming (Dugan and Hubbard 2016)	–	Home/property owner participation (Safford et al. 2014; Scyphers et al. 2014) Shifts in attitude on beach aesthetic (Scyphers et al. 2014)				

Table 1 continued

Case Study (Subsidy)	Possible conservation/restoration strategies			Possible social implications/challenges
	For donor system impacts	For transfer pathway impacts	For recipient system impacts	
Seabirds, Sea Turtles, and Marine Mammals	Federal/international protection of species from exploitation (Call and Loughlin 2005; Moore et al. 2008)	Federal/international protection of nesting/breeding beaches from development (Call and Loughlin 2005) Light pollution regulation (Witherington and Martin 2000)	Remove/exclude introduced predators (Smith et al. 2010; VanderWerf et al. 2014; Jones et al. 2016) Regulate exploitation/guano mining (Wolf et al. 2006) Federal/international protection of species/nests from exploitation (Call and Loughlin 2005)	Regulation of beach and shoreline use/access (Senko et al. 2011)

population sizes, or the complete extirpation of some populations, has led to widespread concern for the subsequent negative effects in the systems (both natural and human) that rely on salmon for nutrient subsidies (Gresh et al. 2000).

Humans affect the transfer of salmon subsidies to riparian systems throughout their life cycle, via both top-down and bottom-up pressures, and therefore moderate the transfer of salmon-derived nutrients as an ecological subsidy in the donor and recipient systems as well as during the transfer between systems (Fig. 1). Within the marine environment, or donor system, direct top-down impacts such as harvesting fish, combined with indirect bottom-up impacts like hatchery fish competition (Levin et al. 2001), lead to a decline in population numbers (Nehlsen et al. 1991), therefore decreasing the availability of the subsidy in freshwater and terrestrial ‘recipient’ systems. Bottom-up pressures along the ecotone, such as habitat modifying hydroelectric dams and other man-made river barriers, often prevent fish from completing their transfer from the marine donor system to spawning streams and subsequent recipient systems (Nehlsen et al. 1991; Gresh et al. 2000; Gende et al. 2002; Freeman et al. 2003). Within the recipient freshwater stream systems, bottom-up impacts such as habitat degradation and competition with farm-raised fish can also decrease the number of successful salmon migrants (Nehlsen et al. 1991). In addition, declines in populations of salmon consumers, such as bears and eagles, via hunting and habitat degradation, indirectly impede the transfer of salmon-derived nutrients to riparian and terrestrial systems from the top-down (Service 1993).

The complex ways in which human activities interact with this economically and culturally valuable subsidy suggests that conservation strategies designed to mitigate reductions in salmon-derived nutrients in recipient systems should also be multifaceted. The need to protect salmon populations and habitat is well established (Gende et al. 2002), and there are a variety of conservation approaches that have been researched or are currently being employed

to varying degrees of success. These approaches include harvest reduction, dam removal, fish ladders, spawning habitat improvement/restoration, artificial fertilization, and salmon-consumer conservation (Table 1).

Beach wrack

Beach wrack is the accumulation of organic detritus (mainly algal debris) deposited directly by waves and tides along the coastal ecotone (Orr et al. 2005) and is a crucial nutrient input to an otherwise nutrient-poor shoreline system (Ince et al. 2007). This ocean-derived subsidy is one of the principle food sources for beach and coastline invertebrates (Crawley et al. 2009; Mellbrand et al. 2011), but also provides marine nutrients to higher trophic levels that feed on macroinvertebrates, such as spiders, seabirds, geckos, lizards, and maritime mammals, such as coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) (Carlton and Hodder 2003; Dugan et al. 2003; Mellbrand et al. 2011). Studies comparing beaches with low or no wrack buildup to beaches with high wrack buildup show that beaches with large volumes of wrack have up to three times higher species abundance, biomass, and richness of epifauna and infauna than beaches with low or no wrack buildup (Dugan et al. 2003; Ince et al. 2007). These findings suggest that a decrease in the quantity of wrack subsidies leads to a decline in beach consumer productivity and diversity, which in turn can result in a decrease in tertiary consumers along the interface.

Human activities can disrupt the subsidy transfer pathway of marine debris to coastal systems within the donor system and along the interface in at least four ways (Fig. 1). First, shoreline armoring, defined as any kind of artificial structure put in place to prevent natural erosion of shoreline sediments (Heerhartz et al. 2014), upsets subsidy transfer via bottom-up mediated influences by preventing it from reaching its recipient system. Armoring can lead to a 66–76% loss in wrack accumulation as it lowers the elevation and narrows the width of beaches on which wrack

accumulates (Heerhartz et al. 2014). Furthermore, armoring is associated with reductions in riparian vegetation and wrack-associated invertebrates (Dethier et al. 2016; Heerhartz et al. 2016), along with changes in subtidal communities (Munsch et al. 2015). Second, beach grooming (a direct top-down impact), or removing wrack from beaches for largely aesthetic reasons (Dugan et al. 2003), prevents the subsidy from entering or accumulating in the recipient system. Third, introduced macroalgae species within the marine ‘donor’ system can influence the composition of beach wrack subsidies as an indirect bottom-up pressure, affecting microbial assemblages (Hahn 2003) and beach invertebrate’s feeding behavior and composition (Bishop and Kelaher 2013a), although these shifts may (Bishop and Kelaher 2013b) or may not affect higher trophic levels and changes in productivity in the same system (Plummer et al. 2013). Similarly, changes within the near-shore marine environment can lead to extreme variability in subsidy deposition and accumulation along the shoreline (Liebowitz et al. 2016). Fourth, climate change may influence wrack subsidies from bottom-up pressures at many points of their transfer, affecting algal growth in the donor system (Krumhansl et al. 2014), altering the nutrient load and chemical defenses of macroalgae when exposed to elevated temperatures and increased ultraviolet radiation in the ocean or on beaches (Rodil et al. 2015), and affecting consumer behavior and abundance within the recipient system (Lastra et al. 2015). Conservation strategies for maintaining beach wrack subsidy transfer are primarily focused on restoring shorelines, removing armoring, discouraging beach grooming, and reducing the presence of invasive species (Table 1).

Seabirds, sea turtles, and marine mammals

Seabirds are well-known vectors of marine-derived nutrient transport to coastal and island ecosystems, feeding within marine systems then depositing their nitrogen- and phosphorus-rich guano within terrestrial systems (Polis and Hurd 1996; Fukami et al. 2006). The presence of this subsidy has been shown to increase the primary productivity of island and coastal ecosystems, alter vegetation composition (Maron et al. 2006; Havik et al. 2014), and increase invertebrate density and diversity (Fukami et al. 2006). In the nutrient-poor waters and coral-derived soils of the tropics, guano can provide essential fuel to entire food webs (Young et al. 2010).

Human activities can have both direct and indirect effects on guano subsidies. Contemporary human activities primarily influence the transfer of these marine subsidies from the bottom-up, indirectly, and within the recipient system (Fig. 1), in the form of seabird disturbance from introduced predators (Croll et al. 2005; Fukami et al. 2006;

Maron et al. 2006; VanderWerf et al. 2014) and from introduced vegetation (Young et al. 2010). The decrease in seabird density in these terrestrial systems due to increased predation or loss of preferred nesting/roosting habitat results in a decrease in subsidy transfer, loss of subsidy availability, and eventual decrease in ecosystem productivity and diversity (Croll et al. 2005; Fukami et al. 2006; Maron et al. 2006; Young et al. 2010). Top-down pressures such as entanglement and bycatch of seabirds in fisheries increases seabird mortality in the donor system and can also reduce guano subsidies. Overall, the most promising conservation strategy already in place is that of introduced predator eradication or exclusion from important nesting sites/areas (Table 1).

Like seabirds, sea turtles and marine mammals are vectors for marine-derived subsidies, transferring nutrients via defecation and mortality while on shore (Bouchard and Bjorndal 2000; Farina et al. 2003; Hannan et al. 2007). Terrestrial consumers that prey upon the adult or juvenile vectors benefit from the additional food source (Lewis and Lafferty 2014), and the increase in nutrient availability from decomposing excrement or carcasses can increase productivity of shoreline vegetation, as well as induce compositional shifts (Hannan et al. 2007). Humans may affect the transfer of these subsidies via these vectors at every point in the exchange (Fig. 1). Within the recipient system, commercial fisheries and pinnipeds may compete, putting bottom-up pressures on pinniped populations and reducing the availability of their excrement as a marine subsidy (Call and Loughlin 2005). As with seabirds, entanglements and bycatch can reduce marine turtle- and mammal-derived subsidies (Lewison et al. 2004; Moore et al. 2008; Lewison et al. 2014), and historically, the direct, top-down impact of exploitation of cetaceans had drastically negative effects on their populations that in turn may have produced far-reaching consequences (Doughty et al. 2015). Cetaceans also have the unique vulnerability of sonar interference (Parsons et al. 2008). Human development along important breeding or nesting shoreline deters vector movement, preventing subsidy transfer and causing further pressure on the vector populations (Bouchard and Bjorndal 2000). Within the recipient system both top-down and bottom-up pressures, turtle nest exploitation, predation by introduced species, and marine mammal carcass removal, further prevent or redirect subsidy transfer (Bouchard and Bjorndal 2000).

The notion of protecting these animals to maintain subsidy vectors is, as of now, not much discussed (but see McLoughlin et al. 2016). However, the idea of protecting sea turtles and marine mammals as vulnerable or endangered species is well established. Thus, the most common conservation strategy to restore marine turtle- and mammal-derived subsidies is akin to that of guano subsidies:

remove or reduce sources of mortality and passively wait for the subsidy to recover. Beyond legal protections of these species at both international (e.g., IUCN) and national levels (e.g., US Marine Mammal Protection Act), other conservation strategies include the protection and restoration of turtle nesting beaches and pinniped colonies (Call and Loughlin 2005), and regulation of light pollution near turtle nesting beaches (Witherington and Martin 2000) (Table 1).

DISCUSSION

Our understanding of ecosystem connectivity via ecological subsidies has increased significantly in the last 20 years. Our examination of the current literature reveals that (1) human activities can affect subsidy movement at any point in the transfer process, including impacts on the donor system, transfer pathway, and recipient system; (2) often human activities have impacts on multiple aspects of the transfer of subsidies; and (3) in many cases, there is limited evidence on the extent to which human impacts influence the subsidy transfer pathway. Clearly, additional research is needed to determine the full extent of human impacts on subsidy transfer pathways to determine the most effective strategies for subsidy conservation and restoration.

While ideally conservation priorities of subsidies should be considered on a case-by-case basis, with the most vulnerable points along the path of transferal being determined, some generalities are apparent. First, direct impacts to subsidies are easier to mitigate than indirect impacts, since indirect impacts are more likely to require management and conservation initiatives that cross sectors. For example, the commercial fishing industry, which has a direct impact on fish populations, is regulated solely by governmental agencies, making management enforcement relatively straightforward. In contrast, the removal of shoreline armoring, which occurs on both private and public land, would require changes to building permitting and beach management policies. Similarly, dam removal to restore salmon runs requires coordinated efforts of agencies charged with terrestrial, freshwater, and in some cases marine, ecosystem management.

Second, conservation measures designed to reduce just one type of impact may not be sufficient to restore a subsidy. Subsidies can be disrupted by human activities in the donor system, in the transfer of the subsidy, or in the disturbance of the transfer vector. Conservation efforts that address only one aspect of subsidy movement may have little effect on the ultimate delivery of the subsidy to the recipient system. Instead, it is likely that a reduction in the cumulative effects of disparate human activities across the full subsidy transfer pathway will offer greater returns.

This can be seen in the example of salmon; efforts to reduce human impacts within the donor system, primarily regulating catch numbers, have been established for decades, and yet stock numbers have not fully recovered from their broad decline during the twentieth century (Ruckelshaus et al. 2002). Additional conservation efforts related to salmon habitat restoration and populations of salmon consumers are needed for these fish populations to survive and prosper in the next century (Nehlsen 1994).

Third, simply reducing the impact on a subsidy may not be enough to restore the ecological structure and function it supported. Even for subsidies where only a single impact type is apparent, such as in the case of seabird guano, there can be other changes in the system that have occurred in parallel to the impacts on the subsidy, such as hysteresis effects (Beisner et al. 2003). For example, the regulation of guano mining is an important first step in conserving the important influx of marine nutrients to island and coastal systems by seabirds, but additional efforts, such as artificial fertilization or seabird colony reintroductions coupled with nesting habitat restorations, may be necessary to restore the lost buildup of subsidy availability.

Our review yields many additional questions and challenges for the conservation of aquatic to terrestrial subsidies as a component of ecosystem-level conservation efforts. In general, these questions relate to the issue of prioritization. While it is ethically challenging and perhaps even impossible to deem one process or ecosystem more important than another, it is pertinent in making initial conservation decisions to hierarchically categorize areas or subsidy pathways most ‘in need’ for protection or restoration (Bottrill et al. 2008). When determining ‘need,’ the cost of managing a subsidy should be evaluated relative to the expected ecological, economic, and sociocultural benefits of doing so. Generating expectations for benefits is non-trivial, but can be accomplished by evaluating the potential sensitivity of the system to different management approaches. For example, sensitivity could be determined based on the relative productivity of systems with and without the subsidy or the historical importance of the subsidy to system food web dynamics. The social value of a subsidy (e.g., the cultural value to native people of restoring salmon runs to the Elwha River (Greaves 2002), or the tourism value of conserving sea turtle populations (Tisdell and Wilson 2001; Wilson and Tisdell 2001)) may also influence the likelihood and ultimate success of restoration (Goldman et al. 2008).

Using such criteria, we expect that the conservation or restoration of some subsidies will be more impactful than others. Systems with a high relative dependence on subsidies to maintain productivity will likely have a quicker response rate at lower costs of intervention, and have short-term benefits that denote their potential long-term

consequences. Similarly, subsidies that have historically been essential to food web dynamics or have high social value will likely be seen as a higher-priority conservation issue. However, while the recipient system may respond quickly to the restoration of a subsidy (Maron et al. 2006), the subsidy itself may be slow to recover, thus impacting the appearance of the overall response rate. Finally, it is important to consider whether some pathways impacted by humans are more tractable than others to conservation or restoration action. This question will be better answered as the field of subsidy and ecotone conservation increases, but the complexity and cost of the management action and the expected effectiveness of the intervention may define the ‘tractability.’ In some cases, the potential impact of management efforts is straightforward. For example, the prevention of wrack accumulation by regular beach grooming may be easier to reverse due to the relative simplicity the conservation or restoration effort required. Others, such as a complete restoration of salmon subsidies, are much more complex, as they will require a multifaceted approach to achieve full recovery and likely require more cost-intensive conservation efforts.

Conservation strategies that aim to protect ecosystem connectivity and subsidy transferal will necessarily be multifaceted, and in many cases, this complexity will require prioritization of different approaches to protect or restore the movement of the subsidy, while also taking into account social pressures and concerns. Full effectiveness may only be achieved if a series of strategies are employed simultaneously, or at least in a well-choreographed manner. Such a plethora of conservation efforts will not only increase subsidy availability but is also likely to improve conditions for other environmental concerns and the integrated human system.

Acknowledgements We would like to thank the Gordon & Betty Moore Foundation for their generous support of the Ocean Tipping Points project, friends and family for their support, and the public library system for its unwavering presence and generous hours wherever/whenever the paper needed to be worked on (especially the Elizabeth C. Miller Library and the public libraries located in Ely, MN, and Fairbanks, AK). We also gratefully acknowledge BHO for his compassion during the development of this paper.

REFERENCES

- Anderson, W.B., and G.A. Polis. 1999. Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* 118: 324–332.
- Baxter, C.V., K.D. Fausch, M. Murakami, and P.L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85: 2656–2663.
- Beisner, B.E., D.T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1: 376–382.
- Bishop, M.J., and B.P. Kelaher. 2013a. Context-specific effects of the identity of detrital mixtures on invertebrate communities. *Ecology and Evolution* 3: 3986–3999.
- Bishop, M.J., and B.P. Kelaher. 2013b. Replacement of native seagrass with invasive algal detritus: Impacts to estuarine sediment communities. *Biological Invasions* 15: 45–59.
- Bottrill, M.C., L.N. Joseph, J. Carwardine, M. Bode, C. Cook, E.T. Game, H. Grantham, S. Kark, et al. 2008. Is conservation triage just smart decision making? *Trends in Ecology & Evolution* 23: 649–654.
- Bouchard, S.S., and K.A. Bjorndal. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* 81: 2305–2313.
- Call, K.A., and T.R. Loughlin. 2005. An ecological classification of Alaskan Steller sea lion (*Eumetopias jubatus*) rookeries: A tool for conservation/management. *Fisheries Oceanography* 14: 212–222.
- Carlton, J.T., and J. Hodder. 2003. Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology Progress Series* 256: 271–286.
- Christie, K.S., M.D. Hocking, and T.E. Reimchen. 2008. Tracing salmon nutrients in riparian food webs: Isotopic evidence in a ground-foraging passerine. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 86: 1317–1323.
- Cline, T.J., D.E. Schindler, and R. Hilborn. 2017. Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nature Communications* 8: 14042.
- Cloern, J.E. 2007. Habitat connectivity and ecosystem productivity: Implications from a simple model. *American Naturalist* 169: E21–E33.
- Compton, J.E., C.P. Andersen, D.L. Phillips, J.R. Brooks, M.G. Johnson, M.R. Church, W.E. Hogsett, M.A. Cairns, et al. 2006. Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. *Frontiers in Ecology and the Environment* 4: 18–26.
- Crawley, K.R., G.A. Hyndes, M.A. Vanderklift, A.T. Revill, and P.D. Nichols. 2009. Allochthonous brown algae are the primary food source for consumers in a temperate, coastal environment. *Marine Ecology Progress Series* 376: 33–44.
- Croll, D.A., J.L. Maron, J.A. Estes, E.M. Danner, and G.V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307: 1959–1961.
- Dethier, M.N., W.W. Raymond, A.N. McBride, J.D. Toft, J.R. Cordell, A.S. Ogston, S.M. Heerhartz, et al. 2016. Multiscale impacts of armoring on Salish Sea shorelines: Evidence for cumulative and thresholds effects. *Estuarine, Coastal and Shelf Science* 175: 106–117.
- Doughty, C.E., J. Roman, S. Faurby, A. Wolf, A. Haque, E.S. Bakker, Y. Malhi, et al. 2015. Global nutrient transport in a world of giants. *PNAS*.
- Dugan, J.E., and D.M. Hubbard. 2016. Sandy Beaches. In *Ecosystems of California*, ed. H. Mooney, and E. Zavaleta, 389–408. Oakland: California, University of California Press.
- Dugan, J.E., D.M. Hubbard, M.D. McCrary, and M.O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal and Shelf Science* 58: 25–40.
- East, A.E., G.R. Pess, J.A. Bountry, C.S. Magirl, A.C. Ritchie, J.B. Logan, T.J. Randle, et al. 2015. Large-scale dam removal on the Elwha River, Washington, USA: River channel and floodplain geomorphic change. *Geomorphology* 228: 765–786.
- Epanchin, P.N., R.A. Knapp, and S.P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. *Ecology* 91: 2406–2415.

- Farina, J.M., S. Salazar, K.P. Wallem, J.D. Witman, and J.C. Ellis. 2003. Nutrient exchanges between marine and terrestrial ecosystems: The case of the Galapagos sea lion *Zalophus wollebaecki*. *Journal of Animal Ecology* 72: 873–887.
- Foley, M.M., J.A. Warrick, A. Ritchie, A.W. Stevens, P.B. Shafroth, J.J. Duda, M.M. Beirne, et al. 2017. Coastal habitat and biological community response to dam removal on the Elwha River. *Ecological Monographs*.
- Freeman, M.C., C.M. Pringle, E.A. Greathouse, and B.J. Freeman. 2003. Ecosystem-level consequences of migratory faunal depletion caused by dams. *Biodiversity, Status, and Conservation of the World's Shads* 35: 255–266.
- Fukami, T., D.A. Wardle, P.J. Bellingham, C.P.H. Mulder, D.R. Towns, G.W. Yeates, K.I. Bonner, et al. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters* 9: 1299–1307.
- Gende, S.M., R.T. Edwards, M.F. Willson, and M.S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* 52: 917–928.
- Gittman, R.K., S.B. Scyphers, C.S. Smith, I.P. Neylan, and J.H. Grabowski. 2016. Ecological consequences of shoreline hardening: A meta-analysis. *BioScience* 66: 763–773.
- Goldman, R.L., H. Tallis, P. Kareiva, and G.C. Daily. 2008. Field evidence that ecosystem service projects support biodiversity and diversify options. *Proceedings of the National Academy of Sciences of the United States of America* 105: 9445–9448.
- Greaves, T. 2002. Examining indigenous rights to culture in North America. *Cultural Dynamics* 14: 121–142.
- Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: Evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25: 15–21.
- Hahn, D.R. 2003. Alteration of microbial community composition and changes in decomposition associated with an invasive intertidal macrophyte. *Biological Invasions* 5: 45–51.
- Hannan, L.B., J.D. Roth, L.M. Ehrhart, and J.F. Weishampel. 2007. Dune vegetation fertilization by nesting sea turtles. *Ecology* 88: 1053–1058.
- Havik, G., A. Catenazzi, and M. Holmgren. 2014. Seabird nutrient subsidies benefit non-nitrogen fixing trees and alter species composition in South American coastal dry forests. *Plos One* 9.
- Heerhartz, S.M., M.N. Dethier, J.D. Toft, J.R. Cordell, and A.S. Ogston. 2014. Effects of shoreline armoring on beach wrack subsidies to the nearshore ecotone in an estuarine fjord. *Estuaries and Coasts* 37: 1256–1268.
- Heerhartz, S.M., J.D. Toft, J.R. Cordell, M.N. Dethier, and A.S. Ogston. 2016. Shoreline armoring in an estuary constrains wrack-associated invertebrate communities. *Estuaries and Coasts* 39: 171–188.
- Helfield, J.M., and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82: 2403–2409.
- Hilderbrand, G.V., T.A. Hanley, C.T. Robbins, and C.C. Schwartz. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121: 546–550.
- Hocking, M.D., and T.E. Reimchen. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos* 118: 1307–1318.
- Hocking, M.D., R.A. Ring, and T.E. Reimchen. 2009. The ecology of terrestrial invertebrates on Pacific salmon carcasses. *Ecological Research* 24: 1091–1100.
- Holtgrieve, G.W., and D.E. Schindler. 2011. Marine-derived nutrients, bioturbation, and ecosystem metabolism: Reconsidering the role of salmon in streams. *Ecology* 92: 373–385.
- Ince, R., G.A. Hyndes, P.S. Lavery, and M.A. Vanderklift. 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. *Estuarine, Coastal and Shelf Science* 74: 77–86.
- Jones, H.P., N.D. Holmes, S.H.M. Butchart, B.R. Tershy, P.J. Kappes, I. Corkery, A. Aguirre-Muñoz, D.P. Armstrong, et al. 2016. Invasive mammal eradication on islands, results in substantial conservation gains. *Proceedings of the National Academy of Sciences of the United States of America* 113: 4033–4038.
- Knight, T.M., M.W. McCoy, J.M. Chase, K.A. McCoy, and R.D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437: 880–883.
- Kohler, A.E., T.N. Pearsons, J.S. Zendt, M.G. Mesa, C.L. Johnson, and P.J. Connolly. 2012. Nutrient enrichment with Salmon Carcass analogs in the Columbia River basin, USA: A stream food Web analysis. *Transactions of the American Fisheries Society* 141: 802–824.
- Krumhansl, K.A., J.-S. Lauzon-Guay, and R.E. Scheibling. 2014. Modeling effects of climate change and phase shifts on detrital production of a kelp bed. *Ecology* 95: 763–774.
- Larsen, S., J.D. Muehlbauer, and E. Marti. 2016. Resource subsidies between stream and terrestrial ecosystems under global change. *Global Change Biology* 22: 2489–2504.
- Lastra, M., J. Lopez, and G. Neves. 2015. Algal decay, temperature and body size influencing trophic behaviour of wrack consumers in sandy beaches. *Marine Biology* 162: 221–233.
- Leroux, S.J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11: 1147–1156.
- Levin, P.S., R.W. Zabel, and J.G. Williams. 2001. The road to extinction is paved with good intentions: Negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society B-Biological Sciences* 268: 1153–1158.
- Lewis, T.M., and D.J.R. Lafferty. 2014. Brown bears and wolves scavenge humpback whale carcass in Alaska. *Ursus* 25: 8–13.
- Lewison, R.L., L.B. Crowder, A.J. Read, and S.A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution* 19: 598–604.
- Lewison, R.L., L.B. Crowder, B.P. Wallace, J.E. Moore, T. Cox, R. Zydelski, S. McDonald, A. DiMatteo, et al. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxaspecific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences of the United States of America* 111: 5271–5276.
- Liebowitz, D.M., K.J. Nielsen, J.E. Dugan, S.G. Morgan, D.P. Malone, J.L. Largier, D.M. Hubbard, and M.H. Carr. 2016. Ecosystem connectivity and trophic subsidies of sandy beaches. *Ecosphere* 7.
- Maron, J.L., J.A. Estes, D.A. Croll, E.M. Danner, S.C. Elmendorf, and S.L. Buckelew. 2006. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. *Ecological Monographs* 76: 3–24.
- Martins da Silva, L.G., L.B. Nogueira, B.P. Maia, and L.B. de Resende. 2012. Fish passage post-construction issues: Analysis of distribution, attraction and passage efficiency metrics at the Baguari Dam fish ladder to approach the problem. *Neotropical Ichthyology* 10: 751–762.
- Massol, F., D. Gravel, N. Mouquet, M.W. Cadotte, T. Fukami, and M.A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14: 313–323.
- McLoughlin, P.D., K. Lysak, L. Debeffe, T. Perry, and K.A. Hobson. 2016. Density-dependent resource selection by a terrestrial herbivore in response to sea-to-land nutrient transfer by seals. *Ecology* 97: 1929–1937.

- Mellbrand, K., P.S. Lavery, G. Hyndes, and P.A. Hamback. 2011. Linking land and sea: Different pathways for marine subsidies. *Ecosystems* 14: 732–744.
- Moore, J.E., B.P. Wallace, R.L. Lewison, R. Zydels, T.M. Cox, and L.B. Crowder. 2008. A review of marine mammal, sea turtle and seabird bycatch in USA fisheries and the role of policy in shaping management. *Marine Policy* 33: 435–451.
- Muehlbauer, J.D., S.F. Collins, M.W. Doyle, and K. Tockner. 2014. How wide is a stream? Spatial extent of the potential “stream signature” in terrestrial food webs using meta-analysis. *Ecology* 95: 44–55.
- Munsch, S.H., J.R. Cordell, and J.D. Toft. 2015. Effects of shoreline engineering on shallow subtidal fish and crab communities in an urban estuary: A comparison of armored shorelines and nourished beaches. *Ecological Engineering* 81: 312–320.
- Nehlsen, W. 1994. Salmon stocks at risk: Beyond 214. *Conservation Biology* 8: 867–869.
- Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific Salmon at the crossroads—Stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16: 4–21.
- Orr, M., M. Zimmer, D.E. Jelinski, and M. Mews. 2005. Wrack deposition on different beach types: Spatial and temporal variation in the pattern of subsidy. *Ecology* 86: 1496–1507.
- Parsons, E.C.M., S.J. Dolman, A.J. Wright, N.A. Rose, and W.C.G. Burns. 2008. Navy sonar and cetaceans: Just how much does the gun need to smoke before we act? *Marine Pollution Bulletin* 56: 1248–1257.
- Pess, G.R., M.L. McHenry, T.J. Beechie, and J. Davies. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Science* 82: 72–90.
- Plummer, M.L., C.J. Harvey, L.E. Anderson, A.D. Guerry, and M.H. Ruckelshaus. 2013. The role of eelgrass in marine community interactions and ecosystem services: Results from ecosystem-scale food Web models. *Ecosystems* 16: 237–251.
- Polis, G.A., and S.D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147: 396–423.
- Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289–316.
- Puth, L.M., and K.A. Wilson. 2001. Boundaries and corridors as a continuum of ecological flow control: Lessons from rivers and streams. *Conservation Biology* 15: 21–30.
- Richardson, J.S., and T. Sato. 2015. Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology* 8: 406–415.
- Richerson, K., and D.S. Holland. 2017. Quantifying and predicting responses to a US West Coast salmon fishery closure. *ICES Journal of Marine Science*.
- Rodil, I.F., P. Lucena-Moya, C. Olabarria, and F. Arenas. 2015. Alteration of macroalgal subsidies by climate-associated stressors affects behavior of wrack-reliant beach consumers. *Ecosystems* 18: 428–440.
- Roni, P., T.J. Beechie, R.E. Bilby, F.E. Leonetti, M.M. Pollock, and G.R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific northwest watersheds. *North American Journal of Fisheries Management* 22: 1–20.
- Ruckelshaus, M.H., P. Levin, J.B. Johnson, and P.M. Kareiva. 2002. The Pacific salmon wars: What science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33: 665–706.
- Safford, T.G., K.C. Norman, M. Henly, K.E. Mills, and P.S. Levin. 2014. Environmental awareness and public support for protecting and restoring puget sound. *Environmental Management* 53: 757–768.
- Schindler, D.E., M.D. Scheuerell, J.W. Moore, S.M. Gende, T.B. Francis, and W.J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* 1: 31–37.
- Schindler, D.E., R. Hilborn, B. Chasco, C.P. Boatright, T.P. Quinn, L.A. Rogers, and M.S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465: 609–612.
- Schulz, R., M. Bundschuh, R. Gergs, C.A. Bruhl, D. Diehl, M.H. Entling, L. Fahse, et al. 2015. Review on environmental alterations propagating from aquatic to terrestrial ecosystems. *Science of the Total Environment* 538: 246–261.
- Scyphers, S.B., J.S. Picou, and S.P. Powers. 2014. Participatory conservation of coastal habitats: The importance of understanding homeowner decision making to mitigate cascading shoreline degradation. *Conservation Letters* 8: 41–49.
- Senko, J., A.J. Schneller, J. Solis, F. Ollervides, and W.J. Nichols. 2011. People helping turtles, turtles helping people: Understanding resident attitudes toward sea turtle conservation and opportunities for enhanced community participation in Bahia Magdalena, Mexico. *Ocean and Coastal Management* 54: 148–157.
- Service, U. S. F. a. W. 1993. *Grizzly Bear Recovery Plan*. Missoula: MT, University of Montana.
- Smith, R.K., A.S. Pullin, G.B. Stewart, and W.J. Sutherland. 2010. Effectiveness of predator removal for enhancing bird populations. *Conservation Biology* 24: 820–829.
- Soininen, J., P. Bartels, J. Heino, M. Luoto, and H. Hillebrand. 2015. Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience* 65: 174–182.
- Stanley, E.H., and M.W. Doyle. 2003. Trading off: The ecological removal effects of dam removal. *Frontiers in Ecology and the Environment* 1: 15–22.
- Thomas, S.M., S.W. Griffiths, and S.J. Ormerod. 2015. Adapting streams for climate change using riparian broadleaf trees and its consequences for stream salmonids. *Freshwater Biology* 60: 64–77.
- Tisdell, C., and C. Wilson. 2001. Wildlife-based tourism and increased support for nature conservation financially and otherwise: Evidence from sea turtle ecotourism at Mon Repos. *Tourism Economics* 7: 233–249.
- Toft, J.D., J.R. Cordell, and E.A. Armbrust. 2014. Shoreline armoring impacts and beach restoration effectiveness vary with elevation. *Northwest Science* 88: 367–375.
- VanderWerf, E.A., L.C. Young, S.E. Crow, E. Opie, H. Yamazaki, C.J. Miller, D.G. Anderson, L.S. Brown, et al. 2014. Increase in wedge-tailed shearwaters and changes in soil nutrients following removal of alien mammalian predators and nitrogen-fixing plants at Kaena Point. *Hawaii. Restoration Ecology* 22: 676–684.
- Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Melillo. 1997. *Human Domination of Earth's Ecosystems Science* 277: 494–499.
- Wilson, C., and C. Tisdell. 2001. Sea turtles as a non-consumptive tourism resource especially in Australia. *Tourism Management* 22: 279–288.
- Witherington, B.E., and R.E. Martin. 2000. Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches.
- Wolf, S., B. Keitt, A. Aguirre-Munoz, B. Tershy, E. Palacios, and D. Croll. 2006. Transboundary seabird conservation in an important North American marine ecoregion. *Environmental Conservation* 33: 294–305.

Young, H.S., D.J. McCauley, R.B. Dunbar, and R. Dirzo. 2010. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proceedings of the National academy of Sciences of the United States of America* 107: 2072–2077.

AUTHOR BIOGRAPHIES

Emily V. Buckner (✉) is an aspiring ecologist and recent graduate of Carleton College. Her research interests revolve around the importance of the movement of energy and nutrients across landscapes in maintaining the healthy function of connected ecosystems. She hopes to pursue a PhD in ecology and conservation biology and career dedicated to exploring sustainable human-ecological relationships.

Address: Department of Biology, Carleton College, 1 North College Street, Northfield, MN 55057, USA.

Address: 3324 E Laurelhurst DR NE, Seattle, WA 98105, USA.

e-mail: embuckner@gmail.com

Daniel L. Hernández is an associate professor of Biology at Carleton College. An ecosystem ecologist, he is currently researching the effects of changes in plant communities (from disturbance, herbivory, and loss of biodiversity) on carbon and nutrient cycling in savannas and grasslands.

Address: Department of Biology, Carleton College, 1 North College Street, Northfield, MN 55057, USA.

e-mail: dhernand@carleton.edu

Jameal F. Samhouri is a marine ecologist and conservation biologist at the NOAA Northwest Fisheries Science Center. His research focuses on how people's activities influence marine ecosystems, and how changes in marine ecosystems affect people.

Address: Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.

e-mail: jameal.samhouri@noaa.gov