Chapter 3
Modification of Habitat Quality by Non-native Species

Jorge L. Gutiérrez

Abstract Non-native species can affect the quality of habitats available to other organisms and, in turn, the ecosystem services they provide or regulate. Although much research to date has focused on the impacts of non-native species on habitats, the links between habitat impacts and the provision or modulation of ecosystem services have remained elusive. This review illustrates two general kinds of non-native species impact on the abiotic conditions and resources available in a habitat: (1) assimilatory-dissimilatory impacts from the uptake and release of energy and materials and (2) physical ecosystem engineering impacts that arise from structural modification of environments caused by species presence and/or activities. Additionally, it distinguishes between physical ecosystem engineering impacts that result from the creation or modification of physical structures per se (e.g., effects on living space) and those that occur because of the interactions of physical structures and different forms of kinetic energy, such as heat or fluid flows (e.g., wind attenuation by trees). Examples are given to illustrate the co-occurrence of multiple impact pathways and their often compound impacts on single habitat attributes. Finally, the habitat-mediated impacts of non-native species on food and raw materials, climate, and tourism and recreation are discussed as examples of cascading impacts on provisioning, regulating, and cultural services, respectively.

Keywords Abiotic conditions • Ecosystem services • Ecological impact • Invasive species • Habitat • Ecosystem engineers • Resources • Physical structures

J.L. Gutiérrez (✉)
Grupo de Investigación y Educación en Temas Ambientales (GrIETA), San Eduardo del Mar, Argentina

Facultad de Ciencias Exactas y Naturales & CONICET, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA
e-mail: jgutierrez@grieta.org.ar

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3.1 Introduction

Non-native species can profoundly alter the habitat available to other organisms (Crooks 2002). In so doing, they can have significant knock-on effects on human well-being because a variety of the benefits that humans derive from ecosystems—or ecosystem services—are contributed or modulated by organisms. Given the dependence of many ecosystem services on the abundance and activity rates of organisms, habitat is often considered as part of the supporting functions or structures (Farber et al. 2006), or simply supporting services on which other kinds of ecosystem services depend. Although impacts on habitats have been largely documented in the literature, the consequences of these effects in the provision or modulation of ecosystem services are nevertheless less appreciated.

This chapter reviews the distinct kinds of non-native species impacts on the quality of habitats available to other organisms. It focuses on the habitat-mediated impacts of these species on food and raw materials, climate, and tourism and recreation as examples of cascading impacts on provisioning, regulating, and cultural services, respectively. Habitat is defined here as the physical place where organisms live (Farber et al. 2006), which includes its physical structure as well as the consumable resources and abiotic conditions that produce occupancy (Hall et al. 1997). In this same vein, habitat quality is defined as the property of the environment to provide the physical structure, consumable resources, and abiotic conditions appropriate for occupancy by a focal species (Hall et al. 1997).

3.2 Impacts on Habitat Quality

Most of the mechanisms that underlie the impact of non-native species on habitats can be broadly classified as assimilation-dissimilation or physical ecosystem engineering impacts (sensu Jones and Gutiérrez 2007). These effects encompass impacts on the physical structures, consumable resources, and abiotic conditions that define habitat quality for other species (Gutiérrez et al. 2014).

Assimilation-dissimilation involves the uptake (assimilation) of energy and materials (e.g., light, water, nutrients, other minerals, O_2, CO_2, trace gases, organic compounds) and their release (dissimilation) in the form of dead tissues and waste products (e.g., carbon and nutrients in litter; woody debris; faeces, urine, and carcasses; water, O_2, CO_2, trace gases, H^+, and other organic and inorganic chemicals). Assimilatory-dissimilatory transfers encompass all kinds of autotrophic, mixotrophic, and heterotrophic interactions (e.g., plant uptake and litter production; herbivory, predation, detritivory, microbial uptake and release).

Physical ecosystem engineering, in contrast, arises from the structural modification of the environment caused by the presence or activities of organisms (Jones et al. 1994). Examples include wind attenuation by trees, animal burrowing, dam-building by beavers, and soil compaction by large mammals. Such structure-mediated

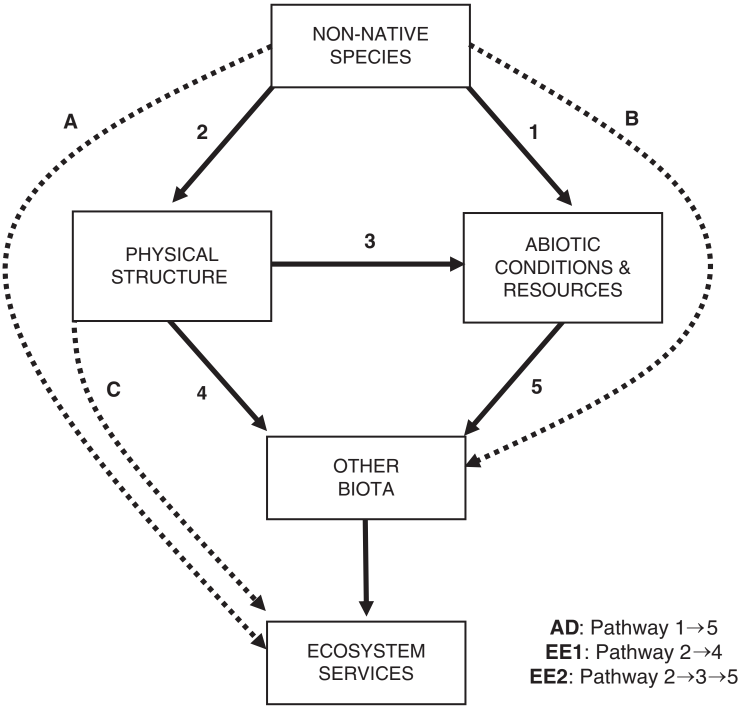

Fig. 3.1 Non-native species impacts on habitat quality and consequences for other ecosystem services. The *solid arrows* represent pathways of impact that involve changes in habitat quality, including assimilatory-dissimilatory (AD) impacts that result from the uptake and release of energy and materials by non-native species, and physical ecosystem engineering (EE) impacts that arise from structural modification of the environment because of the presence or activities of the non-native species. Distinction is made here between engineering impacts that result from the creation or modification of physical structures per se (EE1) and those that occur because of the interactions of physical structures and different forms of kinetic energy, such as heat or fluid flows (EE2). The *dotted arrows* represent non-native species impacts on ecosystem services that occur irrespective of habitat changes, namely, direct assimilatory-dissimilatory impacts (*pathway A*), consumption of organisms involved in the provision or modulation of services (*pathway B*), and direct effects of engineered structures (*pathway C*)

effects are often associated with assimilatory and dissimilatory transfers to varying degrees (e.g., soil reworking by feral pigs when foraging on roots). Nonetheless, the effects of structure on the abiotic conditions and consumable resources available to other organisms cannot be predicted from the nature and magnitude of these transfers alone. Considering the aforementioned example, the effects of feral pigs on soil topography will depend on foraging rates but also on baseline soil properties, vegetation cover, rainfall, and evaporation (Jones and Gutiérrez 2007).

Assimilatory-dissimilatory (AD) and physical ecosystem engineering (EE) pathways of non-native species impact on habitat quality are represented in Fig. 3.1. Assimilation-dissimilation affects habitat quality via changes in resource availability and abiotic conditions that result from the consumption or provision of energy and materials in the form of living or dead tissues and metabolic end-products (AD: pathway 1 → 5 in Fig. 3.1). Ecosystem engineering involves changes on the physical structure of the habitat. Such structural changes may lead to altered habitat quality per se (e.g., availability of physical living space or nesting sites) (EE1: pathway 2 → 4 in Fig. 3.1), or interact with distinct forms of kinetic energy thus altering the abiotic conditions and the availability of consumable resources via dissipation, reflection, and conversion along with material redistribution (e.g., tree effects on understory temperature, flow attenuation, and organic matter deposition in macrophyte beds) (EE2: pathway 2 → 3 → 5 in Fig. 3.1). Impacts on habitat quality via these pathways are outlined next and exemplified in detail in Table 3.1.

3.2.1 Assimilatory-Dissimilatory Impacts on Abiotic Conditions and Consumable Resources

Assimilatory-dissimilatory effects of non-native species on the abiotic conditions and consumable resources available to other organisms can result from the consumption of materials and energy (e.g., food, water, nutrients, light) or their supply in the form of living (e.g., leaves, fruit, animal tissues) or dead matter (e.g., litter, carrion) and metabolic end-products (e.g., faeces, urine, allelochemicals). Effects resulting from material and energy consumption include reduced light levels in the understory of non-native trees (Reinhart et al. 2006), decreased phytoplankton biomass in rivers and lakes as the result of filter feeding by non-native invertebrates (Sousa et al. 2009), and macrophyte biomass decreased by consumption by non-native grazers (e.g., the golden apple snail, *Pomacea canaliculata,* in southeastern Asia wetlands and rice fields; Horgan et al. 2014).

Examples involving the supply of energy and materials include altered organic matter quantity and quality in soils resulting from inputs of non-native plant litter, increased food supply to frugivores caused by the establishment of non-native fruiting plants [e.g., glossy privet, *Ligustrum lucidum,* in the subtropical forests of northwestern Argentina], and toxic water column ammonia levels caused by invasive bivalve die-offs (e.g., *Corbicula fluminea* in southeastern US rivers).

3.2.2 Physical Ecosystem Engineering Impacts on Habitat Structure

A pervasive example of non-native species impact on habitat quality that results from the creation or modification of physical structures per se is the provision of living space to other organisms in aquatic environments, either in the form of hard substrate for attachment or structural refugia against consumers (Jones et al. 2010). Examples include aquatic macrophytes (e.g., the common reed *Phragmites*

Table 3.1 Non-native species impacts on habitat quality and their underlying mechanisms. See Fig. 3.1 for more details and Figs. 3.2 and 3.3 for illustrations

Species (origin)	Case study	Habitat impacts	Mechanism (Pathways)	References
Blue-leafed wattle *Acacia saligna* (Western Australia)	South African fynbos	Soil N and organic matter (+)	Large inputs N-rich litter (AD)	(1)
		Light irradiance and soil temperature (−)	Shading and altered heat transfer (AD-EE2)	(1)
		Water yield in catchments (−)	Root uptake (AD)	(2)
Amur honeysuckle *Lonicera maackii* (China and Japan)	Midwestern US forests	Allelopathy (Q)	Release of allelochemicals (AD)	(3)
		Light irradiance in the forest floor (−)	Shading (AD-EE2)	(4)
		Food supply to some frugivorous birds (+)	Fruit production (AD)	(5)
		Bird nesting sites (+, −, Q)	Altered habitat architecture (EE1)	(6)
Iceplant *Carpobrotus edulis* (South Africa)	Californian coastal scrub	Water availability (−)	Root uptake (AD)	(7)
		Food availability to some mammals (+)	Fruit production (AD)	(8)
		Soil carbon content (+) and pH (−)	Decomposition (AD)	(9)
Smooth cordgrass *Spartina alterniflora* (Atlantic coast of the Americas)	Southeastern China salt marshes	Soil accretion rates (+)	Sedimentation (EE2), and dead-root accumulation (EE1)	(10)
		Food quality for grazing crabs (+)	Biomass production (AD)	(11)
		Space available to ground foraging birds (−)	Preemption by dense canopies (EE1).	(12)
Red seaweed *Gracilaria vermiculophylla* (Northwest Pacific)	Southeastern US estuary mudflats	Food supply to grazers (+)	Biomass production (AD)	(13)
		Food supply to detritivores (+)	Addition of highly decomposable litter (AD)	(13)
		Interstitial space for mobile invertebrates (+)	Formation of dense algal mats (EE1)	(14)
Earthworms *Lumbricus terrestris* and several other species (Europe and Asia)	Northeastern US forests	Surface litter cover (−)	Litter consumption/burial (AD/EE1)	(15)
		Soil porosity (+) and nutrient leaching (+)	Particle aggregation and burrowing (EE1, EE2)	(15)
		Microhabitats to soil arthropods (Q)	Construction of burrows and middens (EE1)	(16)
		Food supply to some consumers (+)	Biomass production (AD)	(16)

(continued)

Table 3.1 (continued)

Species (origin)	Case study	Habitat impacts	Mechanism (Pathways)	References
Gypsy moth *Lymantria dispar* (Eurasia and Northern Africa)	Northeastern US mixed-oak forests	Leaf-litter inputs to soils (–)	Tree defoliation by caterpillars (AD)	(17)
		Inputs of labile C and N to soils (+)	Production of feces or frass (AD)	(17)
		Food base to some birds and mammals (+)	Biomass production (AD)	(18)
		Light penetration to the forest floor (+)	Reduced tree canopy cover (EE2)	(17)
		Runoff and soil erosion (+)	Reduced tree transpiration, increased throughfall (AD-EE2)	(17)
Zebra mussel *Dreissena polymorpha* (Eastern Europe and Central Asia)	Hudson River Estuary, NY, USA	Phytoplankton densities (–)	Filter feeding (AD)	(19)
		Light penetration into water column (+)	Removal of suspended particles (EE2)	(19)
		Interstitial space for mobile invertebrates (+)	Mussel aggregation into dense matrices (EE1)	(19)
		Hard substrate for organismal attachment (+, Q)	Shell production (EE1)	(19)
		Benthic organic matter (+)	Biodeposition (AD)	(19)
Reef-forming polychaete *Ficopomatus enigmaticus* (Australia)	Mar Chiquita Coastal Lagoon, Argentina	Phytoplankton concentrations (–)	Filter feeding (AD)	(20)
		Benthic organic matter (+)	Biodeposition (AD)	(21)
		Hard substrate for organismal attachment (+, Q)	Production of calcareous tubes by worms (EE1)	(22)
		Interstitial space (+, Q)	Reef formation by tube-building worms (EE1)	(23)
		Emergent seabird resting sites (+)	Reef formation by tube-building worms (EE1)	(24)
		Sedimentation (+)	Flow attenuation by reefs (EE2)	(25)
Common carp *Cyprinus carpio* (Eurasia)	Central Mexico shallow ponds	Macrophyte abundance (–)	Grazing (AD)	(26)
		Invertebrate prey (–)	Predation (AD)	(26)
		Sediment resuspension and turbidity (+)	Macrophyte uprooting and sediment reworking (EE2)	(27)

Beaver *Castor canadensis* (North America)	Tierra del Fuego Archipelago, Chile	Riparian forest cover (−)	Foraging and flooding from dam building (AD-EE2)	(28)
		Flow velocities (−)	Dam building (EE2)	(29)
		Sedimentation and benthic organic matter (+, −)	Flow attenuation by dams (EE2)	(29)
Feral pigs *Sus scrofa* (Eurasia)	Hawaii, USA	Food supply to primary consumers (+, −, Q)	Foraging, trampling, uprooting, and tusking (AD-EE1)	(30)
		Water pools in soils and tree trunks (+)	Wallowing and foraging on the pulp of tree ferns (EE2)	(30)
		Soil erosion (+)	Soil reworking and reduced plant cover (EE2)	(30)

Impacts are characterized as quantitative, including increases (+) or decreases (−) in resources or abiotic variables; or as qualitative (Q) when resulting from the generation of resources or abiotic conditions that are novel to some recipient organisms. Mechanisms are classified as assimilatory-dissimilatory (AD), physical ecosystem engineering (EE), and compound ones (AD-EE). Distinction is made between engineering impacts on habitat quality that results from the creation or modification of physical structures per se (EE1), and those that occur because of the interplay between such physical structures and different forms of kinetic energy (EE2)

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australis in northeastern US wetlands) (Kiviat 2013), seaweeds (e.g., the red alga, *Gracilaria vermiculophylla,* in southeastern US estuarine mudflats) (Wright et al. 2014), and sessile invertebrates (e.g., the zebra mussel, *Dreissena polymorpha,* and many other epibenthic bivalves that have become established outside their native range) (see Sousa et al. 2009 for a review).

Other cases include architectural effects of non-native plants on the amount and suitability of nest or perching sites available to birds, and physical restriction of movement in ground-foraging birds by dense, invasive plant canopies (Gan et al. 2009).

3.2.3 Physical Ecosystem Engineering Impacts on Abiotic Conditions and Consumable Resources

The diverse physical effects of non-native plant canopies on abiotic conditions and the fluxes of energy and materials in their understory are chief examples of changes in habitat quality resulting from the interaction between the structures made by non-native species and kinetic energy. The interaction includes light absorption and reflection by canopies which, together with light assimilation (i.e., photosynthesis), can substantially alter irradiance levels in the understory (Reinhart et al. 2006). Non-native plant canopies also dissipate/reflect/convert the energy of fluid flows (wind, water), increasing the deposition of particulate and dissolved matter. The latter is well illustrated by the effects of non-native tree plantations on the deposition of wind-borne sediments (e.g., sand deposition in *Eucalyptus camaldulensis* plantations in Israel; Karschon 1960) as well as pollutants and nutrients (e.g., sulfur and nitrogen deposition in Sitka spruce, *Picea sitchensis*, plantations in northern England; Fowler et al. 1989). Analogous effects occur because of water flow attenuation by macrophytes in aquatic ecosystems (e.g., enhanced sedimentation in *Phragmites australis* marshes in North America; Kiviat 2013).

In addition, the structures built or physically modified by non-native animals can also impact habitat quality by interacting with distinct forms of kinetic energy. Selected examples include non-native earthworm burrows, primarily *Lumbricus terrestris* and *L. rubellus*, that accelerate water infiltration with concomitant increases in nutrient leaching from soils in northeastern US forests (Bohlen et al. 2004); dams built by the introduced beaver, *Castor canadensis,* on Tierra del Fuego Island that attenuate stream flow leading to upstream pond formation, concomitant deposition of suspended sediments and organic matter, and decreased downstream sedimentation (Anderson et al. 2009); and dense networks of burrows made by the non-native isopod *Sphaeroma quoyanum* which weaken salt marsh banks, facilitating their erosion and conversion into unvegetated tidal flats in San Diego Bay and San Francisco Bay, USA (Talley and Crooks 2007).

3.2.4 Compound Impacts on Single Habitat Attributes

As the impacts of plant canopies on understory light irradiance illustrate (see Sect. 3.2.3), non-native species can affect a single habitat attribute via a combination of distinct, concurrent mechanisms, such as photosynthesis and light absorption/reflection. The elimination of riparian forests by beavers in the Tierra del Fuego archipelago also well exemplifies this point, as it occurs because of beaver foraging on seedlings and flooding of the riparian zone as a consequence of dam building (Anderson et al. 2009). Another example in this regard is the development of hypoxia in beds of the floating-leaved macrophyte *Trapa natans* in the shallows of the Hudson River estuary (New York, USA). This species is alleged to deplete oxygen from the water column at least via three mechanisms (Caraco et al. 2006). First, it photosynthesizes in the overlying atmosphere but has substantial amounts of submersed respiratory tissues, which implies that it vents oxygen to the atmosphere to produce organic carbon that, in a significant part, is respired underwater. Second, the dense and thick mats of floating leaves in this species inhibit light penetration and, thus, primary production and oxygen release by other submersed plants. Third, extensive coverage by this species limits the development of turbulence at the air–water interface, thus reducing gas exchange and atmospheric oxygen inputs.

Clearly, the co-occurring mechanisms underlying the compound impacts on a given habitat attribute may not equally be influenced by variations in environmental conditions or the phenological or population status of the species. For instance, early leaf senescence in *T. natans* might have little impact on light penetration and turbulence at the air–water interface but have a significant impact on photosynthesis and respiration. Therefore, recognising these component mechanisms is important to address how their relative contributions drive spatial and temporal variations in overall, compound effects (Gutiérrez et al. 2014).

3.2.5 Concurrent Impacts on Multiple Habitat Attributes

As becomes evident from the examples in Table 3.1, non-native species usually have simultaneous impacts on distinct habitat attributes. They may combine assimilation-dissimilation, physical ecosystem engineering, and compound influences (Table 3.1). Concurrent impacts on habitat attributes can be causally linked (e.g., tree impacts on light regimes and understory temperatures) or bear no apparent relationship to each other (e.g., tree impacts on soil moisture and the availability of nesting sites for birds).

Certainly, not all the habitat attributes concurrently affected by a non-native species are necessarily relevant to a focal species. Yet, apparently insignificant habitat attributes can often mediate impacts on a focal species via complex causal connections. For example, decreases in phytoplankton biomass caused by filter feeding by non-native zebra mussels may be judged beforehand as inconsequential to fishes that feed on benthic and epiphytic invertebrates. Nonetheless, phytoplankton consumption by zebra mussels increases water clarity and the depth of the photic zone, thus increasing the areal cover and biomass of light-limited rooted macrophytes, as well as the abundance of invertebrates that feed on or live amongst these plants and are prey for the fishes in question (Strayer et al. 2004). The foregoing sequence of changes in habitat attributes likely explains increases in invertebrate-feeding littoral fish after zebra mussel invasion (Strayer et al. 2004) and also serves to illustrate that a focus on a single habitat attribute or the most obvious ones affected by non-native species may fall short to characterise changes in habitat quality to focal species, as well as to predict their numerical responses.

3.3 Habitat-Mediated Impacts on Other Ecosystem Services

Non-native species can affect habitat attributes with consequences on the abundance or activity rates of organisms involved in the provision or modulation of other ecosystem services (Figs. 3.2 and 3.3). Such habitat-mediated effects are a subset of the impacts that non-native species can have on ecosystem services. Clearly, many of the impacts of non-native species on ecosystem services occur irrespective of their

Fig. 3.2 Iceplant, *Carpobrotus edulis*, colonizing a coastal dune field in San Eduardo del Mar, Argentina (Photograph by Jorge Gutiérrez)

Fig. 3.3 Reefs built by the non-native polychaete *Ficopomatus enigmaticus* in Mar Chiquita coastal lagoon, Argentina (Photograph by Martín Bruschetti)

effects on the habitat available to other organisms (pathways A–C in Fig 3.2) (see examples in Catford 2017; Fried et al. 2017; Gaertner et al. 2017; Nie et al. 2017). Here, habitat-mediated impacts of non-native species on food and raw materials, climate regulation, and tourism and recreation are examples of cascading impacts on provisioning, regulating, and cultural services, respectively.

3.3.1 Food and Raw Materials

Non-native species affect the quality of habitats of a variety of species that are sources of food and raw materials to humans. In fact, the deliberate introduction of non-native species to enhance habitat quality for such species has been widespread. For instance, there is a long tradition of intentional non-native plant introductions in rangelands to increase forage yield and quality and, ultimately, livestock production. However, there also are several accidentally introduced plants that are unpalatable or toxic to cattle and thus have opposite effects on the quality of rangelands as livestock habitat. Accidentally introduced non-native plants (weeds) can also reduce crop production (Fried et al. 2017) by altering the light environment, consuming soil nutrients, or releasing allelochemicals (Rajcan and Swanton 2001).

The effects of non-native species on habitat attributes also have implications for wild sources of food to humans. For example, freshwater aquatic macrophytes such as the water hyacinth, *Eichornia crassipes,* affect fish habitat in their nonnative ranges by concurrently altering its physical structure (e.g., shelter, space preemption), resources (e.g., prey availability), and abiotic conditions (e.g., oxygen levels). These habitat changes can increase or decrease stocks of commercially important fishes, depending on the requirements of the species in question (Villamagna and Murphy 2010 for a review). Analogous habitat-mediated impacts on economically important fish or shellfish are also documented for marine ecosystems or in response to other habitat-forming non-native species, such as non-native macroalgae or bed-forming bivalves (Jivoff and Able 2003; Strayer et al. 2004).

3.3.2 Climate Regulation

Some non-native species often substantially affect soil physical structure (e.g., aggregate size), resources (e.g., organic matter quantity and quality, N, P), or abiotic conditions (e.g., moisture, redox potential) with consequences for the abundance and activity rates of microorganisms involved in the decomposition of organic matter and the emission of greenhouse gases (Nie et al. 2017). These habitat modifications contributed to increased CO_2 emissions as agriculture and non-native crops expanded across the globe (Lal 2004). However, the net contribution of soil modification by crops to CO_2 emissions is generally hard to separate from the effects of crop management (e.g., tillage, fertilizer, and pesticide use).

The impacts of soil habitat modification by non-native species on microbial processes and greenhouse gas emissions are particularly well documented in wetlands, whose primarily anaerobic soils are a favourable habitat for microbes that decompose organic matter into methane. Non-native plants in wetlands can either increase (Mozdzer and Megonigal 2013) or decrease (Grand and Gaidos 2010) methane emissions. Such changes can be attributed to altered root biomass, productivity, and oxygen release rates and, thus, altered availability of organic carbon or electron acceptors (e.g., oxygen and ferric iron), which jointly regulate the total amount of anaerobic microbial respiration and methane production in soils (Sutton-Grier and Megonigal 2011). Given that wetlands contribute about a third of global methane emissions, widespread non-native plant establishment in wetlands might be significant vis-à-vis climate impacts.

A striking impact on the habitat of methane-producing microbes is that of the beaver, which creates wetlands via dam building. Methane emissions associated with non-native beaver ponds in the Tierra del Fuego archipelago are estimated to amount to about 2.7 Gg $year^{-1}$ (Whitfield et al. 2015). Other impacts of non-native animals on greenhouse gas emissions from soils or sediments include enhanced CO_2 and methane emissions from tidal flats after oyster establishment, which likely results from increases in sedimentary organic carbon from biodeposition and enhanced sedimentation amongst oyster shells (Green et al. 2012); or earthworm-induced increases in CO_2 and N_2O emissions, which partially result from local enrichment of mineral N, available C, and moisture in casts and burrow walls (Lubbers et al. 2013). Although the contributions of these animals are apparently minor at the global scale, they might represent important regional sources of gas emissions.

3.3.3 Tourism and Recreation

Non-native species often cause habitat-mediated impacts on the abundance of charismatic species that are an attraction for ecotourism, such as the Atlantic puffin, *Fratercula arctica*, in Scotland and the critically endangered Montserrat oriole, *Icterus oberi*, on Montserrat Island. Breeding success and size in colonies of the Atlantic puffin have been negatively affected by the spread of non-native tree mallows, *Lavatera arborea*, (Fischer and van der Wal 2007). Similarly, nesting sites for Montserrat orioles have been lost as a consequence of livestock foraging on their primary nesting plants (Peh et al. 2015). Some non-native macrophytes also have habitat-mediated impacts on fish species that are targets of recreational fishing (Slipke et al. 1998).

3.4 Conclusions

This review outlines and exemplifies the general mechanisms of non-native species impacts on habitat quality and the impacts of such habitat changes on other ecosystem services. The habitat-mediated impacts of non-native species on ecosystem services seem to be underreported in the literature relative to their overall impacts on habitat quality. This lack is likely because much of the research on the impacts of non-native species on habitats has been motivated by an interest in the conservation of species and communities, and their habitats, in spite of the services that the species in question may provide. A greater understanding of the links between habitats, species, and ecosystem services, as presented in this review with regard to habitat modification by non-native species, can contribute to a full picture of the costs and benefits of anthropogenic habitat transformation.

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