13 Impacts of Invasive Species on Ecosystem Services

Heather Charles and Jeffrey S. Dukes

13.1 Introduction

The impacts of invasive species on ecosystem services have attracted worldwide attention. Despite the overwhelming evidence of these impacts and a growing appreciation for ecosystem services, however, researchers and policymakers rarely directly address the connection between invasions and ecosystem services. Various attempts have been made to address the ecosystem processes that are affected by invasive species (e.g., Levine et al. 2003; Dukes and Mooney 2004), but the links between these mechanisms and ecosystem services are largely lacking in the literature. Assessments of the economic impacts of invasive species cover costs beyond those associated with ecosystem services (e.g., control costs), and generally do not differentiate by ecosystem service type. Additionally, while advances have been made in quantifying non-market-based ecosystem services, their loss or alteration by invasive species ~~are~~ often overlooked or underappreciated.

Ecosystem services are the benefits provided to human society by natural ecosystems, or more broadly put, the ecosystem processes by which human life is maintained. The concept of ecosystem services is not new, and there have been multiple attempts to list and/or categorize these services, especially as the existence of additional services has been recognized (e.g., Daily 1997; NRC 2005). For the purposes of this chapter, we address ecosystem services in the framework put forward by the Millennium Ecosystem Assessment (2005). The services we list are primarily those enumerated in the Millennium Ecosystem Assessment (2005), with minimal variation in wording, and inclusion of several additional services not explicitly stated in this assessment. This framework places services into four categories (in italics). *Provisioning services* are products obtained from ecosystems, and include food (crops, livestock, fisheries, etc.), freshwater, fiber (timber, cotton, silk, etc.), fuel, genetic resources, biochemicals/pharmaceuticals/natural medicines, and ornamental resources. *Regulating services* are obtained from the regulation of ecosystem

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processes, and include air quality regulation, climate regulation, water regulation (timing and extent of flooding, runoff, etc.), water purification, waste treatment, disease regulation, natural pest control, pollination, erosion control, and coastal storm protection. *Cultural services* are non-material benefits, and include aesthetic values, recreation/tourism, spiritual/religious values, educational/scientific values, cultural heritage values, inspiration, and sense of place. *Supporting services* are overarching, indirect, and occur on large temporal scales, but are necessary for the maintenance of other services. They include photosynthesis, primary production, nutrient cycling, water cycling, soil formation and maintenance of fertility, as well as atmospheric composition. This framework includes both goods, which have direct market values, and services that in turn maintain the production of goods and biodiversity, and directly or indirectly benefit humans (Daily 1997).

In this chapter, we introduce concepts associated with the valuation of ecosystem services, and discuss how costs generated by invasions relate to impacts on ecosystem services. We link the effects of invasive species on community dynamics and ecosystem processes to effects on ecosystem services. Risks for specific ecosystem types and the organism types most likely to change particular services are discussed. Finally, we present examples of invasive species that alter each of these services. While the majority of these species negatively affect ecosystem services, several exceptions exist. We conclude by assessing the overall vulnerability of each category of ecosystem service to alteration by invasive species, suggesting future research needs, and discussing educational and collaborative opportunities in this field.

13.2 Relating Costs of Invasives to Valuation of Ecosystem Services

13.2.1 Valuing Ecosystem Services

In order to understand how invasive species affect ecosystem services, one must first understand how ecosystem services are valued, and how these values relate to the costs of invasive species. Economic valuation of ecosystem services (and goods) typically involves several components. All goods and services are categorized within a framework of total economic value (Fig. 13.1), and subsequently assigned monetary value (Costanza et al. 1997).

The framework initially differentiates between use and non-use values. Use values further divide into direct and indirect use values. Direct use values involve human interaction with nature, and include both consumptive and non-consumptive uses. Consumptive use refers to products consumed locally or sold in markets, whereas non-consumptive use typically refers to cultural

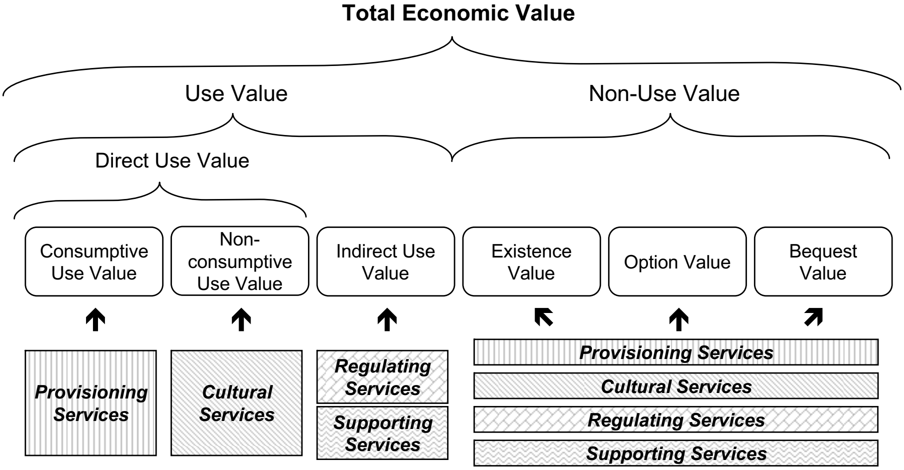

Fig. 13.1 Framework for economic valuation of ecosystem services (see text for further explanation)

services such as recreation and tourism. Indirect use values encompass species that humans rely on indirectly through trophic and other interactions (e.g., natural pest control), and services that are closely tied to ecosystem processes. Examples are productive inputs such as soil fertility, pollination, water purification, and flood control, all of which are extremely important in agriculture. Non-use values, while less tangible, are critical to a comprehensive assessment of economic valuation. They derive from the continued existence and intrinsic value of a service, good, species, habitat, etc., and include existence, option and bequest values.

These three values are succinctly explained by an example taken from Daily (1997), where non-use values for a hypothetical freshwater site include the value of knowing the site exists, irrespective of whether or not an individual visits the site (existence value); the value of preserving the option of enjoying the site in the future (option or future use value); and the value of ensuring that one's descendants will be able to enjoy the site (bequest value). While the literature on ecological economics includes several variations of this framework, all versions include the same basic principles (e.g., Daily 1997; NRC 2005; Born et al. 2005).

We link the total economic value framework to our discussion of ecosystem services and invasive species in two ways. First, the categories of ecosystem services can be connected to the categories of valuation in a generalized manner (Fig. 13.1). Provisioning services, which include all goods, fall into the consumptive use category. Most cultural services are considered to have non-consumptive use values. Regulating and supporting services are typically classified as having indirect use values. As mentioned above, the framework can include multiple values for a service, and thus all four categories of services can be assessed for their non-use value as well. For example, genetic resources and certain plant/animal species may have an option value for future medicines and gene therapy targets, both provisioning services. Endangered species and locations with high endemism, such as the Galapagos Islands, may have a high existence value and a correspondingly high tourism value. Sites or species with spiritual, religious, or cultural importance may have a significant bequest value, owing to their cultural services.

Second, with a measure of the value of an ecosystem service available, it is easier to assess the magnitude of alteration by invasive species. Invasives pose threats to human society that are proportional to the value of the services they threaten. Overall, because ecosystem services are defined by their contribution to human society, the significance of any alteration due to invasive species is dependent on their valuation. However, it should be noted that services may be undervalued if they are poorly understood or underappreciated.

13.2.2 Interpreting Invasive Impacts

Invasive impacts or costs are often classified as economic, environmental, or social in nature. Economic impacts are those of direct consequence to humans, typically leading to monetary losses. Environmental impacts are those that affect ecosystem structure and function, often referring to loss of biodiversity or unique habitats. Social impacts focus predominantly on human health and safety, but can also cover quality of life, recreational opportunities, cultural heritage, and other aspects of social structure. Where do ecosystem services fit into this classification? A unique facet of the concept of ecosystem services is the conjoining of ecological integrity and human benefit. As such, impacts will fall into all three categories with a good deal of overlap. Thus, all three types of impacts are useful in determining which services are affected by invasive species, and the magnitude of these effects.

Economic impact assessments give clues to some of the most significant impacts to humans by way of ecosystem services, but two caveats exist. First, economic assessments include control and management costs that are critical in determining control vs. prevention strategies, but do not address ecosystem services. Second, and more pertinent, economic assessments do not fully assess the alteration of certain ecosystem services, due to their subjective nature and the difficulty of assigning value. This includes almost all supporting services, and many regulating and cultural services. Since market values are easier to assign, and changes to these values are felt sooner and more acutely, economic assessments are necessarily biased toward provisioning services. Environmental impact assessments cover many of these remaining services, but often indirectly (e.g., biodiversity itself is not an ecosystem service per se), and without connections made to human benefits lost or gained.

Social impact assessments cover a smaller range of services, and some are not tied to ecosystem services (e.g., invasive insects that bite humans).

Nevertheless, we can make a few generalizations from impact assessments. Impacts of invasive species on ecosystem services related to agriculture, industry, and human health are substantial, well quantified, and typically negative (Chap. 18). These impacts affect the delivery of food, freshwater, and fiber, as well as water purification, pollination, natural pest control, disease regulation, soil fertility, and nutrient and water cycling. Invasives are having substantial, if not fully quantified, impacts on cultural services including aesthetic values, recreation, and tourism, in both riparian and upland areas (Eiswerth et al. 2005). Decreased biodiversity and species extinctions linked to invasive species threaten the continued delivery and quality of many ecosystem services. Finally, negative alterations of ecosystem services far outweigh positive alterations. Chapter 19 provides further discussion of economic and social impacts, as well as methods of impact assessment. Table 13.1 lists several studies that have quantified invasive species' impacts on specific ecosystem services, and includes both positive and negative impacts.

Table 13.1 Monetary impacts to ecosystem services associated with various invasive species

Invasive species	Geographic location	Ecosystem services altered	Monetary impact[a]	Reference
Acacia melanoxylon (blackwood), *Acacia cyclops* (rooikrans), *Eucalyptus* spp. (gum trees) and other woody shrubs and trees	Cape Floristic Region, South Africa (fynbos)	Food (sour figs, honeybush tea), fiber (thatching reed, timber), ornamental resources (flowers, greens, ferns), medicine, essential oils (buchu)	−2,852,984[b]	Turpie et al. (2003)
		Water (mountain catchments)	−67,836,059[b]	
		Pollination (bee keeping)	−27,783,728[b]	
		Ecotourism	−830,683[b]	
		Fuel (*Acacia cyclops* as firewood)	+2,799,492[b]	
Bemisia tabaci (whitefly)- and *B. tabaci*-transmitted viruses	Mexico	Food (melon, sesame), fiber (cotton)	−33 million	Oliveira et al. (2001)
	Brazil	Food (beans, tomatoes, melon, okra, cabbage)	−5 billion (for 5–6 years)	
	Florida, USA	Food (tomato, due to *Tomato mottle virus*)	−140 million	
	North America, Mediterranean Basin, Middle East	Food (lettuce, sugar beets, melon, due to *Lettuce infectious yellow virus*)	−20 million	

Table 13.1 (*Continued*)

Invasive species	Geographic location	Ecosystem services altered	Monetary impact[a]	Reference
Melaleuca quinque-nervia	South Florida, USA (wetlands, open-canopied forests)	Recreation (park use)	−168 to 250 million	Serbe-soff-King (2003)
		Tourism (Everglades National Park and rest of south Florida)	−250 million to 1 billion	
		Natural hazard regulation (increased fires)	−250 million	
		Various cultural services (endangered species loss)	−10 million	
		Ornamental resources (nurseries)	−1 million	
		Food (honey production)	+15 million	
Myriophyllum spicatum (Eurasian watermilfoil)	Western Nevada and northeast California; Truckee River watershed, USA	Recreation (swimming, boating, fishing, etc.)	−30 to 45 million	Eisworth et al. (2000)
		Water quality, water supplies, non-use value	Unquantified negative costs	
Pomacea canaliculata (golden apple snail)	Philippines (rice systems)	Productivity losses (rice output)	−12.5 to 17.8 million	Naylor (1996)
Sus scrofa (feral pig)	Florida, USA (three state parks; forest and wetland)	Habitat degradation (with implications for recreation, tourism, aesthetics, endangered species loss, erosion control, water quality)	−5,331 to 43,257 ha^{-1}, depending on park, season, and ecosystem type	Engeman et al. (2003)
Tamarix spp. (tamarisk)	Western United States, especially Colorado River	Irrigation water	−38.6 to 121 million	Zavaleta (2000)
		Municipal water	−26.3 to 67.8 million	
		Hydropower	−15.9 to 43.7 million	
		Natural hazard regulation (flood control)	−52 million	

[a] Costs are indicated with a negative sign (−) and benefits with a positive sign (+). Values are in US $ and represent annual losses, unless otherwise indicated

[b] Values were converted from 2,000 Rands (R) to US $; 7 R=1 $

13.3 Mechanisms of Alteration

Ecosystems are characterized by their structure (composition and biological/physical organization) and functions or processes, which lead to the production and maintenance of ecosystem services. Invasive species alter the production, maintenance, and quality of services by a variety of mechanisms. As understanding of invasion biology has increased, so too has recognition and comprehension of these mechanisms. The mechanisms are interrelated, since they all affect aspects of the defining characteristics of ecosystem structure and function. However, they can be grouped into three categories to enhance ease in understanding (Fig. 13.2).

13.3.1 Species Extinctions and Community Structure

Invasive effects on native biodiversity and community structure are well known, but few studies have examined the mechanisms that lead to these effects (Levine et al. 2003). Invasive species may alter community structure through exploitation competition (indirect interactions such as resource use), and interference competition (direct interactions such as allelopathy in plants; Callaway and Ridenour 2004). Invasive impacts on other species interactions, including predation, herbivory, parasitism, and mutualisms, can change the abundance of species with certain key traits that influence ecosys-

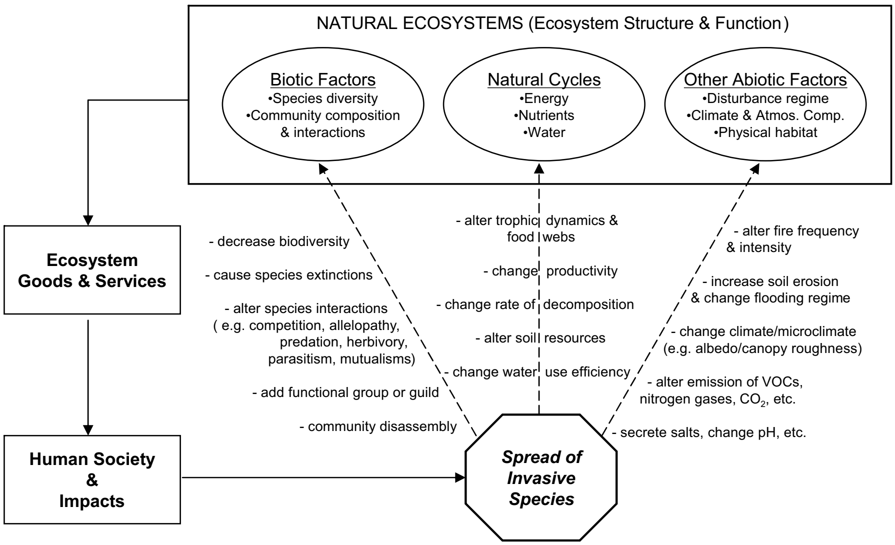

Fig. 13.2 Mechanisms of ecosystem service alteration by invasive species

tem processes (Chapin et al. 2000). A handful of nonnative animals, plants, and pathogens have also been implicated in extinctions of native species, in particular invasive animals on islands.

Changes in species and community structure can affect ecosystem services both directly and indirectly. Direct effects include the decline in abundance of economically valuable species, in particular those used for food, forage, fiber, fuel, or medicine. Aesthetic values are commonly lost with the arrival of "nuisance species" such as invasive vines or aquatic floating plants. Invasives that disrupt mutualisms pose risks particularly for pollination and natural pest control services. Decreased genetic diversity and species extinctions also lead to loss of option value. For example, the brown tree snake (*Boiga irregularis*) is blamed for the extinction of multiple bird and other species in Guam, with negative impacts on tourism, and unknown costs in genetic resources (Fritts and Rodda 1998). Indirect effects include a potential decrease in ecosystem resistance and resilience to change, due to the hypothesized link between stability and changes in biodiversity (Hooper et al. 2005). Finally, positive feedbacks due to interactions of invasive species may lead to increased vulnerability to further invasion, and potential degradation of ecosystem services (Simberloff and Von Holle 1999).

13.3.2 Energy, Nutrient and Water Cycling

Invasive species' impacts also operate at the ecosystem level through the alteration of natural cycles. Energy flows can be altered by changes in trophic interactions, food webs and keystone species. For example, the herbivore *Pomacea canaliculata* (golden apple snail) has dramatically decreased aquatic plant populations in wetlands in Southeast Asia. This in turn has led to the dominance of planktonic algae, high nutrient levels, high phytoplankton biomass, and turbid waters, with implications for water quality and purification (Carlsson et al. 2004). Productivity can be altered by invasive species that use resources more efficiently, or that eliminate a prominent life form (Dukes and Mooney 2004). Since primary productivity is itself an ecosystem service, this shift could be detrimental to humans. Changes in decomposition rate, such as might occur if an invasive species altered litter chemistry, can affect nutrient cycling as well.

Nutrient cycling can also be altered by invasive plants that fix nitrogen, leach chemicals that inhibit nitrogen fixation by other species, release compounds that alter nutrient availability or retention, including nitrogen and phosphorus, and alter topsoil erosion or fire frequency (Dukes and Mooney 2004). The best studied of these mechanisms is the introduction of leguminous species with mutualistic nitrogen-fixing microorganisms, largely due to the dramatic effects of the invaders *Myrica faya* (fire tree) in Hawaii, New Zealand and Australia, and *Acacia mearnsii* (black wattle) in South Africa

(Levine et al. 2003). Ehrenfeld (2003) has shown that invasive plant impacts on nutrient cycling can vary in magnitude and direction across both invader types and sites, indicating that patterns are not universal, and that effects on ecosystem services can be either positive or negative. Alteration of nutrient cycling has additional implications for maintenance of soil fertility and primary production.

Invasive plant species have been shown to alter hydrological cycles by changing evapotranspiration rates and timing, runoff, and water table levels. Impacts are greatest when the invaders differ from natives in traits such as transpiration rate, leaf area index, photosynthetic tissue biomass, rooting depth, and phenology (Levine et al. 2003). Changes to water cycles may affect both water supply and regulation. Well-studied examples of invasive plants using more water than do native plants, and thus decreasing the water supply for humans, include *Tamarisk* spp. (salt cedar) in riparian zones of the southwestern United States, and pines in the Cape region of South Africa.

13.3.3 Disturbance Regime, Climate, and Physical Habitat

Several invasive species alter disturbance regimes (including fire, erosion, and flooding), or act as agents of disturbance themselves, particularly in soil disturbance (Mack and D'Antonio 1998). Fire enhancement can occur when grasses invade shrublands and increase fire frequency, extent, or intensity, whereas fire suppression is more likely to occur when trees invade grassland^ and decrease fine fuel load and fire spread (Mack and D'Antonio 1998). These impacts are significant since they can cause a shift in ecosystem type and related species – for example, from shrublands to grasslands. Affected ecosystem services might include air purification or quality, atmospheric composition (e.g., through increased nitrogen volatilization), forage quality for cattle, and primary production. Mammalian invaders often increase erosion and soil disturbance, whereas woody plant invaders are more likely to affect water regulation by causing flooding and sedimentation in aquatic settings.

Maintenance of climate and atmospheric composition, both ecosystem services, are two of the least-studied mechanisms, perhaps because changes can occur over large temporal and spatial scales. Hoffmann and Jackson (2000) used modeling simulations to show that conversion of tropical savanna to grassland could both reduce precipitation and increase mean temperatures. However, the impetus for this study was land use change, not invasive species per se. On a smaller scale, experiments have shown that even a handful of invasive plants can alter a given microclimate. Finally, invasive species may alter atmospheric composition by changing rates of carbon dioxide sequestration, or the emission of volatile organic compounds and other biologically important gases (Dukes and Mooney 2004). Huxman et al. (2004) note that CO_2 and water flux to the atmosphere will be affected by the species-specific soil microclimate, and show differences in these fluxes between native and invasive grasses.

Invasive species can also alter the physical habitat. Both plant and animal invaders are capable of outcompeting natives and taking over habitat, and certain invaders additionally make the habitat less suitable for other species. Invasive plants may decrease the suitability of soil for other species by secreting salts (e.g., *Tamarisk*, Zavaleta 2000; the iceplant *Mesembryanthemum crystallinum*, Vivrette and Muller 1977), by acidifying the soil, or by releasing novel chemical compounds, as in allelopathy (Callaway and Ridenour 2004).

13.4 Which Ecosystems are at Risk and Which Invasives have the Greatest Impact?

Predicting which invasive species will have the greatest impact on ecosystem services would have both economic and societal benefits, and allow us to improve our prevention and management strategies. Unfortunately, the relationships between ecosystem impacts and ecosystem service impacts are difficult to characterize. We expect that species with the greatest ecological impacts will also have the greatest impacts on ecosystem services, but this has not been tested. Likewise, the relationship between community invasibility and the intensity of impacts is also debatable (Levine et al. 2003). Some generalizations can be made regarding the species most likely to alter ecosystem processes. Invasives that add a new function or trait have the potential to significantly impact ecosystem processes as their ranges expand, often by the addition of a new functional type based on traits related to resource use (e.g., nitrogen fixers), phenology, feeding habits, habitat preference, etc. (Chapin et al. 1996). Even without the addition of a new function or trait, an invader that comprises a large proportion of the biomass at a given trophic level may measurably alter ecosystem structure and function (Dukes and Mooney 2004). Invasive species of all taxa are capable of altering ecosystem services.

Which invasive species might pose the greatest threat to a given ecosystem service in a given system? This question is difficult to answer; few concrete patterns exist, and we currently rely on a handful of species-specific examples. We can broadly say that specific ecosystem types are susceptible to alteration of particular ecosystem services (Table 13.2). For simplicity, we use the six ecosystem types delineated by The State of the Nation's Ecosystems (The H. John Heinz III Center for Science Economics and the Environment 2002): coasts and oceans, farmlands, forests, fresh waters, grasslands and shrublands, and urban and suburban areas. These generalizations are necessarily subjective, based on our review of the literature. One notable source of information on a broad range of invader taxa and habitat and ecosystem types is the Global Invasive Species Database (http://www.issg.org/database).

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Table 13.2 Ecosystem types differ in ecosystem services most at risk and prevalent invasive species types

Ecosystem type	Ecosystem services most at risk	Prevalent invader types	Invader examples and impacts	Other
Coasts and oceans	– Commercial fisheries – Shellfish beds – Water purification – Waste treatment – Disease regulation – Recreation, tourism	– Alga, seaweeds – Mollusks – Crustaceans – Fish	Caulerpa seaweed (*Caulerpa taxifolia*) – Forms dense mats in Mediterranean Sea – Negative impacts on aquaculture/fishing (Verlaque 1994) Green crab (*Carcinus maenus*) – Consumes native commercially important clams in Tasmania (Walton et al. 2002)	– Isolated areas more susceptible (e.g., Mediterranean and Black seas) – Long-distance dispersal makes eradication difficult
Farmlands and croplands	– Natural pest control – Pollination – Nutrient cycling – Primary production	– Insects – Pathogens – Grasses – Forbs – Birds	Sweet potato whitefly (*Bemisia tabaci*) – Consumes crops, transmits plant viruses and fungi; affects crops and ornamentals (Oliveira et al. 2001) Banana bunchy top virus – Invades tropical Asia, Africa, Australia by vector aphid; damages fruit (Dale 1987)	– Large economic losses can result from introduced pests and crop-specific pathogens
Forests	– Timber – Nonwood products – Genetic resources – Ornamental resources – Aesthetic value	– Fungal pathogens – Forbs – Shrubs and vines – Insects – Mammals	Chestnut blight (*Cryphonectria parasitica*) Dutch elm disease (*Ophiostoma ulmi*) White pine blister rust (*Cronartium ribicola*) – Species–specific fungal pathogens with negative aesthetic and genetic impacts	– Subsistence economies at risk due to dependence on forest products (Daily 1997)

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Table 13.2 (*Continued*)

Ecosystem type	Ecosystem services most at risk	Prevalent invader types	Invader examples and impacts	Other
Fresh waters (rivers, streams, lakes, ponds, wetlands, riparian)	– Water purification – Water regulation – Erosion control – Disease regulation – Recreation, tourism	– Aquatic plants – Fish – Mollusks – Amphibians	Zebra mussel (*Dreissena polymorpha*) – Threatens water supply, quality and native clams following rapid dispersal through Great Lakes (Griffiths et al. 1991) Whirling disease (*Myxobolus cerebralis*) – Threatens trout in rivers in the USA, with impacts on recreation (Koel et al. 2005)	– Isolated lakes very susceptible – Rivers and riparian areas difficult to control; can easily transport propagules
Grasslands and shrublands (including desert and tundra)	– Livestock forage – Genetic resources – Air quality regulation – Nutrient cycling – Cultural heritage	– Grasses – Forbs – Shrubs – Trees – Mammals	Starthistle (*Centaurea solstitialis*) – Decreases livestock forage yield and quality, and depletes soil moisture (Gerlach 2004) Mesquite (*Prosopsis glandulosa*), *Acacia* spp. – Alter nitrogen and carbon cycling in arid lands worldwide (Geesing et al. 2000)	– Invasive species have decreased rangeland quality in many regions of the world
Urban and suburban	– Disease regulation – Aesthetic value – Cultural heritage	– Weedy plants – ~~Nuisance species~~ – Birds – Pathogens	House mouse (*Mus musculus*) Norway rat (*Rattus Norvegicus*) Grey squirrel (*Sciurus carolinensis*) – Can spread disease, and decrease aesthetic value by invading fragmented landscapes	– Close proximity of humans adds to adverse impacts on disease regulation

13.5 Case Studies and Examples

13.5.1 Provisioning Ecosystem Services

We have identified a range of examples of invasive species that covers a substantial breadth of services, species, and locations. Provisioning services are perhaps the easiest to assess, since impacts occur on a shorter time scale and are often felt more acutely, at least initially, than for other services. Crops are negatively impacted by invasives eating them, such as the European starling (*Sturnus vulgaris*) feeding on grain and fruit crops such as grapes (Somers and Morris 2002), and by decreases in land productivity and agricultural yields. Livestock are impacted indirectly by invasives that decrease forage quality or quantity, such as the unpalatable leafy spurge (*Euphorbia esula*) avoided by cattle in the mid-western United States (Kronberg et al. 1993), or directly by pathogens such as rinderpest, which is fatal to cattle and has led to famines in many parts of the world. Although many economically important crop and livestock species are invasive, they are typically under human management.

Marine food resources can be impacted by invasive predators such as the European green crab (*Carcinus maenus*; Table 13.2), and by competition with invasives such as the comb jelly (*Mnemiopsis leidyi*), which has devastated fisheries in the Black Sea as well as other seas (Shiganova et al. 2001). Impacts of invasives on water resources are among the best studied, particularly in the South African fynbos. Water is a critical resource in this semiarid region, and multiple invasive species, including *Melia azedarach*, pines, wattle (*Acacia mearnsii*), mesquite (*Prosopis* spp.) and *Lantana camara*, have substantially decreased available surface water and streamflow through their high evapotranspiration rates (Gorgens and van Wilgen 2004).

Timber and other structural support materials are particularly susceptible to termite (*Coptotermes* spp.) damage in South America (Constantino 2002) and other parts of the world. Fuel resources such as wood presumably share the same threats. Cotton and other fiber crops are susceptible to various invasive agricultural pests such as the red imported fire ant (*Solenopsis invicta*), which consumes beneficial arthropods (Eubanks 2001). Ornamental resources, especially trees, are susceptible to attack, and even death from the aphid *Cinara cupressi* throughout Europe and Africa (Watson et al. 1999), as well as from pathogens such as *Phytophthora* spp. It is important to note that many invasive plants have been introduced because they have ornamental value, despite negative impacts they may now have caused. Finally, due to their high option value, genetic resources, biochemicals, pharmaceuticals, and the like are at risk whenever there is a loss of biodiversity. Invasives that lead to species extinctions, such as the small Indian mongoose (*Herpestes javanicus*) or the rosy wolf snail (*Euglandina rosea)*, may irretrievably alter these services. In addition, invasions into hotspots of biodiversity such as the tropics and aridlands pose significant risks to current and future sources of these provisioning services.

13.5.2 Regulating Ecosystem Services

Invasive species also alter regulating services, with far-reaching effects on human society. Fires release particulates, carbon monoxide and dioxide, and nitrogen oxides, leading to decreased air quality. Thus, invasives such as cheatgrass (*Bromus tectorum*) that increase fire frequency will enhance these emissions. In addition, several invasive plants, including kudzu (*Pueraria montana*) and eucalyptus, emit large amounts of isoprene, which is highly reactive in the atmosphere and enhances the production of air pollutants (Wolfertz et al. 2003). Emission of isoprene and other volatile organic compounds also leads to the production of ozone and greenhouse gases such as carbon monoxide and methane, thereby altering climate regulation. On a smaller scale, invasives may alter microclimates. For example, smooth cordgrass (*Spartina alterniflora*) reduces light levels in salt marsh plant canopies, potentially decreasing estuarine algal productivity (Callaway and Josselyn 1992).

Invasives generally have a negative effect on water regulation. Salt cedar (*Tamarix* spp.) forms thickets along riparian corridors enhancing sediment capture and channel narrowing. This has decreased the water holding capacity of many waterways in the southwestern United States, leading to more frequent and extensive flooding and associated flood control costs (Zavaleta 2000). Water purification occurs in multiple types of ecosystems, but most notably in wetlands. The common carp (*Cyprinus carpio*) has been shown to decrease water quality in a degraded wetland in Spain by increasing turbidity and nutrient concentrations (Angeler et al. 2002). Aquatic invasive plants and mollusks may also impact waste treatment by clogging water pipes.

Disease regulation is altered by the invasion of human disease pathogens themselves (e.g., *Vibrio cholerae*, cholera-causing bacteria), or the invasion of disease vectors, particularly invasive mosquitoes such as *Aedes aegypti*, native to Africa, which enhanced the spread of yellow fever in the Americas and of dengue in tropical Asia (Juliano and Lounibos 2005). Natural pest control and pollination are well studied, due to wide recognition of their high economic value. Pest control is altered directly by invasives that consume or compete with either beneficial or detrimental insects, and indirectly by invasives that harbor additional pests. This complicated role is illustrated by the red imported fire ant (*Solenopsis invicta*), an intraguild predator that consumes both insect pests of soybeans and native biological control agents (Eubanks 2001). Impacts on pollination are equally complex. Honey bees (*Apis mellifera*) have been introduced worldwide for pollination services, but research suggests they may competitively displace native bee faunas, which are typically better pollinators (Spira 2001). Invasive plants may also threaten pollination services by luring pollinators from native species, as was shown with *Impatiens glandulifera* in central Europe (Chittka and Schurkens 2001).

Alteration of erosion control is linked to a large number of invasives. Despite the fact that many invasives were originally introduced to dampen erosion, many in fact increase erosion. Examples range from large mammals such as feral pigs (*Sus scrofa*), which uproot plants, disturb soil, and are particularly damaging on islands (Mack and D'Antonio 1998), to small invertebrates such as the isopod *Sphaeroma quoyanum*, which has increased marsh erosion in California due to its burrowing activities (Talley et al. 2001). Since marshes also protect coasts from natural hazards, including hurricanes and strong waves, this loss of sediment is likely to decrease this service as well.

13.5.3 Cultural Ecosystem Services

Alteration of cultural services is far more difficult to assess, given the subjective nature of these services. For example, purple loosestrife (*Lythrum salicaria*) may actually increase the aesthetic value of wetlands for some observers, due to its brightly colored profusion of flowers, whereas others might find the sight distasteful, given their concerns about the species' effects on water quality and wildlife habitat provision. By the same token, the ability of natural ecosystems to provide inspiration is very personal and has the potential to change over time, even for one individual. In addition, the specific cultural, spiritual, religious, or other values held by an individual or group may be unknown. Nevertheless, the impacts of many invasives can be assumed to apply to a majority of individuals. For example, aesthetic values are lost during intense Asian gypsy moth (*Lymantria dispar*) invasions into forests in the northeastern United States, due to defoliation and corresponding high tree mortality (Hollenhorst et al. 1993). Invaders also cause substantial losses to recreation and tourism, particularly ecotourism. Aquatic macrophytes that form dense layers or beds are a notorious nuisance for boating, swimming, and diving. Examples are found worldwide in both fresh and salt water, and include *Caulerpa taxifolia*, *Hydrilla verticillata*, and *Sargassum muticum* (cf. Global Invasive Species Database). Terrestrial invasive plants may also form dense stands crowding out native species, and impacting recreation and tourism by making natural areas less accessible and by potentially reducing wildlife and rare-plant viewing. Examples include *Melaleuca quinquenervia*, *Mimosa pigra*, Japanese knotweed (*Fallopia japonica*), and the cactus *Opuntia stricta* (cf. Global Invasive Species Database).

Several invasives have provided positive recreation and tourism opportunities, especially in the area of fishing. These include large mouth bass

(*Micropterus salmoides*), brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*; Global Invasive Species Database). To put this in perspective, however, most of these invasives cause damage to other ecosystem services. Educational values are certainly lost whenever species become extinct, particularly in areas with high endemism such as the Galapagos Islands, considered a natural laboratory for evolutionary studies. Several endemic plants are considered to have disappeared from these islands due to *Lantana camara* invasion (Mauchamp et al. 1998). Overall, we conclude that all cultural services are altered by invasive species, with some positive effects, but predominantly negative effects. Despite the challenge in placing monetary values on these services, it is critical to recognize their widespread influence.

13.5.4 Supporting Ecosystem Services

Invasive species also directly alter supporting services. These impacts can be elusive, since they occur on large temporal and spatial scales to services not used directly by humans (i.e., they have non-use value). However, supporting services are necessary for the maintenance of all other services – when invasive species alter these, they often alter other, supported services. Thus, most of the examples given in Sects. 13.3.2 and 13.3.3 are not only mechanisms of alteration by invasive species, but also impacts on supporting services. A few additional examples are presented here. Studies of direct alteration to photosynthesis are limited in number. Aquatic plants that form floating mats, such as water hyacinth (*Eichhornia crassipes*), can decrease macroinvertebrate abundance by blocking light transmission and decreasing photosynthesis by phytoplankton and other plants, leading to anoxic conditions (Masifwa et al. 2001). Primary production may increase or decrease if an invasion leads to a shift in the major vegetation type of an area. In many cases, invasive plants increase net primary productivity, as is the case with giant reed (*Arundo donax*) and *Phragmites* in marshes (Ehrenfeld 2003). However, a recent study of buffelgrass (*Pennisetum ciliare*), which has been introduced to the Sonoran desert in Mexico to serve as cattle forage, shows that converted areas have lower net primary productivity than areas with native desert vegetation (Franklin et al. 2006).

Soil formation may be indirectly affected by changes in decomposition rates, soil carbon mineralization, and geomorphological disturbance processes (e.g., erosion), as well as succession (Mack and D'Antonio 1998). Maintenance of soil fertility is directly connected to nutrient cycling. Japanese barberry (*Berberis thunbergii*) and Japanese stilt grass (*Microstegium vimineum*), which have invaded forests in the eastern United States, can significantly alter microbial communities, leading to changes in nitrification and increased soil nutrient concentrations (Ehrenfeld 2003). Finally, atmospheric composition can be altered by changes in net ecosystem carbon exchange.

Reduced carbon sequestration rates in sagebrush communities invaded by annual grasses (Prater et al. 2006) will contribute to climate warming, illustrating the linkages among these global changes (Chap. 12).

13.6 Conclusions

Across invader taxa, ecosystem types, and geographic locations, invasive species are capable of altering ecosystem services by affecting populations, community interactions, ecosystem processes, and abiotic variables. Virtually all ecosystem services can be negatively impacted by invasive species, although positive impacts do exist. Many invasive species cause cascading effects in communities and/or affect both biotic and abiotic components of ecosystems. This usually leads to an influence on multiple ecosystem services. Different ecosystem types are susceptible to the alteration of specific services. Option values illustrate how invasive species may impact future ecosystem services by threatening native species and communities.

Our assessment found a general lack of work in the area of invasive species and their alteration of ecosystem services. To date, scientific research has focused largely on predicting invasibility, comparing invader and native traits, and assessing environmental impacts, particularly on biodiversity. Ecological economics has generally addressed a limited number of ecosystem services, namely, those with direct market valuation. More recently, several papers have examined the causal mechanisms underlying invasive species impacts. These studies have begun to link invasive species, ecosystem structure and function, and ecosystem goods and services. Several studies also hint at impacts to ecosystem services, but do not directly address these services. Research in this area is critical for several reasons. First, impact assessments for invasive species are not complete without considering implications for human society. Comprehensive assessments allow us to better predict impacts, particularly for species in similar taxa. Second, this research has the potential to increase our understanding of invasive impacts on ecosystem structure and function outside the domain of ecosystem services. Because invasive species' impacts on ecosystem services overlap with environmental impacts (e.g., altered biodiversity), scientists will gain knowledge relating to impacts on all native species. This may also lead to advances in understanding invasibility and community interactions. Third, increased awareness of invasive species' impacts could inform decisions on allocating resources for the control of invasives, and for the protection of ecosystem services and "natural" ecosystems. Finally, increased research efforts will be critical in predicting the effects of invasive species in conjunction with other global changes, including climate and land use, which have been shown to affect ecosystem service supply (Schroter et al. 2005). Dialogue between ecologists, economists, and policymakers is critical to moving this research agenda forward.

The four categories of ecosystem services provide a useful framework for assessing our overall knowledge of invasive species' impacts on ecosystem services. Table 13.3 gives a qualitative assessment of several aspects of these four types of services, and suggests a path forward by identifying areas currently lacking research. In particular, supporting and regulating services both have a high value, but a low level of research. Given that their susceptibility to invasive impacts is uncertain and high, respectively, this is evidently an area where research is needed. Recognition of the value of ecosystem services, and the many examples and mechanisms by which invasive species affect ecosystem services lead to several additional opportunities. The general public is still largely unaware of the extent of invasive species' impacts. In addition, society does not often appreciate the extent of its dependence on natural ecosystems (Daily 1997). This creates an opportunity to educate the general public about both issues in tandem, leading to better understanding and appreciation for both. Specific examples of alteration to ecosystem services will also allow policymakers and land managers to prioritize eradication and control campaigns. As with many unquantified threats to human society attributable to global changes, it would be prudent to err on the side of caution in estimating and managing the threats posed by invasive species (i.e., the precautionary principle). As our understanding of the links between invasive species, ecosystem structure and function, and provision of ecosystem goods and services increases, so too will our ability to recognize invasive species' impacts on ecosystem services, and to better manage these impacts.

Table 13.3 Qualitative assessment of the value of ecosystem services and current knowledge of their susceptibility to, and the amount of research focused on, invasive species impacts

Services	Provisioning	Regulating	Cultural	Supporting
Value	High	High	Medium	Very high
Susceptibility to to alteration by invasive species	High	High	Medium to low	Uncertain
Amount of research on invasive impacts	Medium	Low	Medium	Very low

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