# Measuring the Effects of Invasive Plants on Ecosystem Services: Challenges and Prospects

# Measuring the Effects of Invasive Plants on Ecosystem Services: Challenges and Prospects

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Plant invasions can have large effects on ecosystem services. Some plant invaders were introduced specifically to restore key services to ecosystems, and other invaders are having unintended, detrimental effects on services, such as the quantity and quality of water delivered, flood control, erosion control, and food production. Many ecosystem services are difficult to measure directly, and although there are extensive studies on plant invaders and ecosystem processes, a number of challenges prevent us from confidently extrapolating those processes as proxies for services. To extrapolate local, short-term measures of processes to ecosystem services, we must: (1) determine which processes are the key contributors to a service, (2) assess how multiple processes interact to provide a given service, (3) determine how vegetation types and species affect those processes, and (4) explicitly assess how ecosystem services and their controls vary over space and time, including reliance of ecosystem services on ''hot spots'' and ''hot moments'' and a minimum size of a vegetation type in the landscape. A given invader can have positive effects on some services and negative effects on others. It is important to consider that, in some systems, shifting environmental conditions may no longer support native species and that invasive species may be critical contributors to the resilience of ecosystem services.

**Key words:** Carbon sequestration, climate regulation, context dependence, ecosystem processes, erosion control, invader effects, net primary productivity, nutrient supply, plant community composition, resilience, soil fertility, spatial scale, temporal scale, water supply, water quality.

Ecosystem services are the benefits that humans derive from ecosystems, such as food and water provisioning, air and water purification, and control of erosion, pests, and disturbance regimes (Chan et al. 2005; Diaz et al. 2007; Millennium Assessment 2005; Naidoo and Ricketts 2006). Global to regional assessments have demonstrated that human-accelerated environmental changes, including changes in land use and biological invasions, are compromising the delivery of most of these services and making them more susceptible to sudden collapse (Millennium Assessment 2005). Accordingly, it is imperative to improve our understanding and management of multiple services, not only enhancing the delivery of services, but also their resilience (the ability to withstand and recover from a disturbance or environmental change) (Carpenter et al. 2001).

Kremen (2005) highlighted the complex interactions that govern ecosystem services, and the challenge of measuring services over space and time, emphasizing several key components that need to be explicitly addressed to enhance our understanding of the provision of services:

- Which species are the key service providers or degraders?
- At the landscape level, how does the ecological community interact to provide the resilience of a service (e.g., through species that functionally compensate for the loss of a key service provider)?
- What are the key environmental controls over the service?
- What are the spatiotemporal scales over which providers and services operate?

It has been well documented that the composition of the biotic community affects services (Bennett et al. 2009; Kremen 2005; Luck et al. 2009), leading to concerns over potential effects of invasive species on human well-being. These effects on ecosystem services are increasingly being used as criteria for prioritizing efforts to remove or manage invasive plants (Sieg et al. 2010). There are many high-profile case studies on how invasive plants can result in unintended decreases in ecosystem services (Charles and

## Management Implications

There is increasing interest in managing for multiple ecosystem services, but ecosystem science cannot yet provide the information needed by managers to select management approaches that can reliably provide a given service at a given site, or even to reliably measure the effects of management practices on some services. Few studies have quantified the effects of invasive species on ecosystem services (the benefits provided to humans), although many have documented effects on ecosystem processes, which are the fundamental drivers of services. In order to use ecosystem processes as proxies for estimating ecosystem services, we must:

1. Understand which processes are key contributors to a service
2. Assess how multiple processes interact to provide a service
3. Determine how vegetation types and species affect those processes, and
4. Understand how ecosystem services and their controls vary over space and time.

This approach will improve our ability to measure and predict the effects of invasive plants, improving our criteria for prioritizing invasive species management. It is important to consider that invaders can have positive effects on some services and negative effects on others, relative to native species. Invasive species may degrade some systems, but in others, shifting environmental conditions may no longer support native species, making invasive species critical contributors to the resilience of ecosystem services.

Dukes 2007; Pejchar and Mooney 2009). For example, 73% of crop weed species are exotic, leading to an estimated decrease in crop yields by 9%, costing an estimated $23.4 billion annually (Pimentel et al. 2000). Invasion of exotic plants into western U.S. rangelands have decreased range productivity 23 to 75% and, in some cases, decreased soil carbon stores (reviewed in Eviner et al. 2010). Invasion of shrubs and trees into the South African fynbos has greatly decreased water provisioning in a system already highly limited by water (Le Maitre et al. 1996, Mark and Dickinson 2008; van Wilgen et al. 1992). Invasion of riparian areas by tamarisk (*Tamarix* spp.) throughout the southwestern United States has altered stream channel morphology, leading to increases in flood frequency and severity (reviewed in Zavaleta 2000). A number of plant invaders can increase fire frequency, area, and intensity (D'Antonio and Vitousek 1992; Mack et al. 2000) or enhance the prevalence of other pest species (Mack et al. 2000). A global meta-analysis revealed that, although individual invasions may vary in the magnitude and direction of their ecosystem effects, plant invasions have greatly compromised native diversity by decreasing the abundance (by 43.5%), diversity (by 50.7%), and fitness (by 41.7%) of resident plant species and the fitness (by 16.5%) and abundance (by 17.5%) of animal species (Vila et al. 2010).

Although focus on invader effects has largely highlighted negative effects on ecosystem services, many invasive plants were introduced to provide key services (Pimentel et al. 2000). For example, kudzu [*Pueraria montana*

(Lour.) Merr. var. *lobata* (Willd.) Maesen & S.M. Almeida] was introduced for erosion control in the southeastern United States (Forseth and Innis 2004), and in Papua New Guinea, spiked pepper (*Piper aduncum* L.) is planted to increase crop yields by decreasing excess soil moisture and increasing soil nutrients (Hartemink 1999). Invasive plants have also frequently been planted to enhance production of food, timber, or fiber (Richardson 1988). Although these invasive species do provide some benefits, all of these examples have also come at the cost of decreases in native diversity, often far beyond the boundaries of the original plantings (Mack et al. 2000). Some invasives can provide some benefits, at the expense of other services. For example, the introduction of kudzu for erosion control efforts has resulted in decreased air quality (Hickman et al. 2010). The effects of invasive species on ecosystem services may also depend on scale. For example, a number of local studies have shown that invasive plants decrease pollination of native plants (Brown et al. 2002), but at a landscape scale, the high prevalence of invaders can enhance pollinator populations (reviewed in Bjerknes et al. 2007). Although the benefits provided by an invasive species often result in trade-offs of other services, these trade-offs may be justified in extremely altered landscapes. For example, severe degradation of abiotic conditions may limit self-recovery or assisted restoration of the native community, in which case, the exotic species may be the most effective recovery agent to establish plant cover to minimize erosion, provide nurse sites for native plants, or facilitate phytoremediation (Ewel and Putz 2004). For example, in New Zealand, the exotic mouseear hawkweed (*Hieracium pilosella* L.) increases soil organic matter and thus productivity in overgrazed pastures (Scott et al. 2001). Invasions of exotic species may also be a symptom of shifting environmental conditions that will no longer support the native community, a concept known as *novel ecosystems*. In the case of novel systems, invasive species may not be disrupting ecosystem services but may be sustaining them under a shifting environment (Hobbs et al. 2009).

Although it is clear that certain invasive species can have significant effects on specific ecosystem services, we are still far from being able to predict which plant invaders are likely to have marked effects on specific services and to what extent the effect of a given invader may depend on its environment (Figure 1). Many studies have shown that the effect of a given invasive species varies over space and time (Devitt et al. 1998; Ehrenfeld 2003; Eviner and Hawkes 2008). There has also been considerable debate about whether certain invaders affect a given ecosystem service. For example, although many studies have suggested that invasive species, such as tamarisk, decrease water flow through their high evapotranspiration rates, others have challenged those findings,
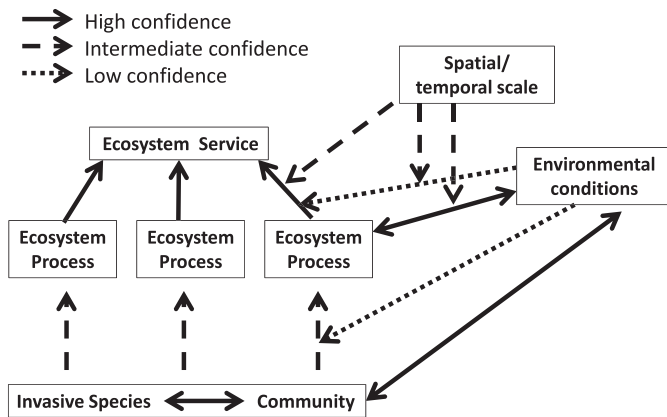
Figure 1. Conceptual diagram illustrating our current strengths and weaknesses in reliably predicting the effects of invasive species on ecosystem services. Solid arrows indicate relationships in which we have strong predictive frameworks, including the suites of ecosystem processes that can potentially contribute to an ecosystem service, the reciprocal effects of environmental conditions and ecosystem processes, the reciprocal effects of environmental conditions and plant community interactions, and interactions between invasive species and their resident communities. Solid, but still developing, conceptual frameworks are denoted by dashed arrows and include effects of plant communities (and invasive species) on ecosystem processes, effects of temporal and spatial scales determining which environmental conditions regulate ecosystem processes, determination of ecosystem processes that contribute to an ecosystem service, and the effects of environmental conditions on which ecosystem processes contribute to a service. Our weakest conceptual models are depicted by dotted lines and include how environmental conditions alter the ecosystem effects of plant communities and how environmental conditions alter which ecosystem processes contribute to a service.

suggesting that measurements were taken at the wrong scale and led to inappropriate and unrealistic conclusions (Owens and Moore 2007). Predicting the effect of a given invader on a given ecosystem service is particularly challenging because we currently know little about the mechanisms by which invasive plants affect services (Charles and Dukes 2007; Pejchar and Mooney 2009), and our current measures of most ecosystem services are still crude (Bennett et al. 2009; Naidoo et al. 2008). This lack of understanding about how to predict and manage, or even measure, the effects of invasive species on ecosystem services limits our ability to effectively prioritize and manage invasions.

This article reviews the challenges that limit our ability to assess the effects of invasive species on ecosystem services and suggests research approaches needed to improve our understanding of the effects of invasive plant species on ecosystem services (Figure 1), highlighting links among ecosystem services, the interaction of multiple ecosystem processes that provide those services, and the spatial and temporal variations in the controls over ecosystem services and processes. We do not focus on valuation, but rather, on approaches for improving quantification of ecosystem services, a critical first step for valuation (Kroeger et al. 2009).

## The Challenge of Measuring Ecosystem Services

Ecosystem services are difficult to measure directly (Bennett et al. 2009; Kremen 2005; National Research Council 2004). Most ecosystem service assessments acknowledge that the current evaluations are based on imperfect indicators (Carpenter et al. 2006; Millennium Assessment 2005; Naidoo et al. 2008). Ideally, ecosystem services would be assessed with long-term, large-scale data; however, these data often don't exist (Carpenter et al. 2006). Furthermore, ecosystem service indicators generally vary by ecosystem type and across scales, making comparisons difficult (Feld et al. 2009). Despite the limitations of our current approaches, they provide critical first steps in identifying threats to services and potential approaches for managing services.

Current assessments of ecosystem services mostly rely on relatively crude calculations. For example, water supply is often calculated as the difference between precipitation and evapotranspiration (e.g., Chan et al. 2006), even though water supply is greatly affected by water infiltration, runoff, and soil storage capacity (Brauman et al. 2007). Water supply can be directly measured, but watershed-scale studies are expensive and rare. Proxy measures for water supply (e.g., evapotranspiration rates of natives vs. exotics) can be heterogeneous in space and time and often don't match actual measures of water supply (Devit et al. 1998; Huxman et al. 2005). Similarly, carbon storage is estimated as plant biomass carbon (e.g., Chan et al. 2006), even though meaningful, long-term carbon storage is dominated by soil storage (Lal 2004). Direct measures of soil carbon storage can be challenging because soil carbon is spatially heterogeneous, even at local scales (Zhu et al. 2010). Measurements of services are particularly challenging because many ecological processes are governed by "hot spots" or "hot moments" (McClain et al. 2003). For example, flood control may only be important during a 100-yr storm. Water quality may be strongly affected by hotspots on the landscape— for example, small wetland areas where denitrification occurs (Verhoeven et al. 2006).

In many ecosystem services assessments, services are inferred based on land use/land cover, even though that relationship is untested in most regions of the world (Bennett et al. 2009; Egoh et al. 2009), and a number of studies have shown that a given land cover conversion (e.g., grassland to woodland) can result in opposite effects on services at different sites (Jackson et al. 2002; reviewed in Eviner and Chapin 2003; Eviner and Hawkes 2008). More-accurate estimates are available for the services that can be

directly measured (e.g., timber or crop production through remote sensing, or stream flow from watersheds) or those that have been well studied over the long term (e.g., forage production). For example, compared with models for typical ecosystem services, forage production models are based on more variables (e.g., climate, net primary production [NPP], forage quality, grazing tolerance, sales of livestock products), which have been calibrated with long-term, large-scale data (Chan et al. 2006; Rinella and Luschei 2007). Our knowledge of these services is relatively well developed in comparison to the large number of services that are less amenable to direct measure.

Few studies have directly measured the effects of plant invasions on ecosystem services. However, there is a rich and growing literature, accompanied by conceptual frameworks, on the effects of invasive species on ecosystem processes (reviewed in Chapin et al. 1997; Ehrenfeld 2003, Eviner and Chapin 2003; Liao et al. 2008; Parker et al. 1999; Strayer et al. 2006; Vila et al. 2010), which are key drivers of ecosystem services.

### Relationship between Ecosystem Processes and Ecosystem Services

*Ecosystem services* are the benefits humans derive from ecosystems (e.g., water supply, air and water purification, pollination, provision of food and fiber), whereas *ecosystem processes* are the conversion or movement of matter or energy resulting from interactions between organisms and their environments (e.g., evapotranspiration, decomposition, nutrient cycling, water infiltration and storage, NPP) (Wallace 2007) (Box 1). Ecosystem processes and services are closely related, but services differ from processes in some key ways:

- Services often integrate across multiple ecosystem processes and attributes (Table 1) (Brauman et al. 2007; Charles and Dukes 2007).

- Measures of ecosystem processes are usually at the plot or patch scales. When considered at larger scales (e.g., watershed), processes are usually considered to be heterogeneous across patch types, rather than integrated into a single, large-scale estimate. In contrast, ecosystem services are often quantified at larger scales, across patch types (e.g., water export from the entire watershed). When ecosystem services are considered at smaller-scale patches within a landscape, it is to identify specific locations that will provide services (e.g., nutrient filtration in stream buffers) or to consider the minimum size of a patch type that will provide a service (Jack et al. 2008).

- The distribution of services depends on the distributions of ecosystem processes and human demands for the service. For example, wetlands or flood plains that may contribute to flood control may not be located in the areas where humans most need flood control. For the purposes of this article, we will focus only on the ecological potential for providing services.

- Although research on both processes and services is increasingly considering the interactions among multiple processes or services, research on services particularly emphasizes the importance of trade-offs, synergies, and interactions among multiple services (Bennett et al. 2009).

Invasive plant effects on ecosystem processes are the key mechanism by which they affect ecosystem services (Charles and Dukes 2007), and our ability to predict and manage the effects of invasive plants on ecosystem services would advance greatly if we could forge better linkages among ecosystem processes and services. The rich literature and strengthening conceptual frameworks toward predicting which invasive plants are likely to affect ecosystem processes can serve as a strong foundation for understanding services. Currently, there are large gaps in our ability to infer services from a given process. In the rest of this article, we discuss how to build on our current knowledge to enhance our ability to predict and manage invasive effects on ecosystem services (Figure 1).

### Challenges in Using Measures of Ecosystem Processes as Proxies for Services

**Integrating Effects of Multiple Ecosystem Processes.** The ability to use an ecosystem process as a proxy for an ecosystem services will depend largely on the multiple processes that interact to produce a service (Table 1) (Brauman et al. 2007; Charles and Dukes 2007; Kremen 2005; van der Putten et al. 2004). Brauman et al. (2007) reviewed the contribution of several hydrologic processes to water supply. Water supply is affected by many individual processes: precipitation, fog and cloud interception, infiltration, canopy interception and evaporation, transpiration, surface runoff, flow attenuation by vegetation, and

Table 1. The ecosystem processes that affect services; the plant traits, environmental factors, and other organisms that affect those processes; and the scales at which they act.[a,b]

| Ecosystem service | Ecosystem processes and attributes that contribute to service | Spatial scale | Important traits of species that act as "key providers" | Other key interacting variables | Key environmental factors |
|---|---|---|---|---|---|
| Water quantity | Water holding capacity (soil organic matter, pore space) | Local | Tissue chemistry, biomass, root structure | Soil invertebrates Herbivores Soil microbes | Soil Climate Topography |
| | Evapotranspiration | Local to regional | Water use efficiency, biomass, leaf area, rooting depth in relation to water sources | Herbivores | Soil Climate Groundwater |
| | Infiltration vs. runoff compaction vegetation cover soil aggregation soil pore space water flow path (e.g., channelization) | Local to regional (depends on water flow) | Root structure Root turnover Canopy structure Root exudates | Soil invertebrates Herbivores Soil microbes | Soil Climate Topography |
| Water quality | Nutrient sequestration | Local to regional, with high heterogeneity at many scales | Tissue chemistry, exudation, uptake | Soil microbes Soil invertebrates Herbivores | Soil Climate Topography |
| | Nutrient cycling | | Tissue chemistry, allocation, exudation, effects on microclimate | Soil microbes Soil invertebrates Herbivores | Soil Climate |
| | Nutrient leaching | | Plant uptake, exudation, water use | Soil microbes Soil invertebrates Herbivores | Soil Climate Topography |
| | Detoxification | | Tolerance, sequestration or ability to chemically convert | Soil microbes | Soil Climate |
| | Erosion control vegetation cover water runoff vs. infiltration soil cohesion soil layers | | Root structure, canopy structure, root turnover and exudates | Soil microbes Soil invertebrates Herbivores | Soil Climate Topography |
| Climate regulation | Latent vs. sensible heat flux | Local to regional | Canopy cover, evapotranspiration, rooting depth | | Climate Soils Topography |
| | Albedo | Local to global | Canopy reflectance Canopy structure Vegetation cover | | Climate Topography |

Table 1. Continued.

| Ecosystem service | Ecosystem processes and attributes that contribute to service | Spatial scale | Important traits of species that act as "key providers" | Other key interacting variables | Key environmental factors |
|---|---|---|---|---|---|
| | Carbon sequestration: Organic matter formation/accumulation (inputs, turnover, transformation of C forms) | Local to global | High root allocation Tissue quality Rooting depth Exudation | Soil microbes Herbivores | Climate Soils Topography |
| | Greenhouse gas emissions | Local to global | See traits that affect nutrients, C, water | Herbivores Soil microbes | Climate Soils |
| Production of food, fiber, timber, forage, etc. | Net primary production | Local to regional, with high heterogeneity at many scales | Growth rate, water use efficiency, nutrient use efficiency, light use efficiency | Soil invertebrates Herbivores Soil microbes | Climate Soils Topography |
| | Nutrient cycling | | Tissue chemistry, allocation, exudation, effects on microclimate | Soil microbes Soil invertebrates Herbivores | Climate Soils |
| | Erosion control | | Root structure, canopy structure, root turnover and exudates | Soil microbes Soil invertebrates Herbivores | Soil Climate Topography |
| | Pest/pathogen control | | Tissue chemistry, tissue turnover time, induced defenses, phenology | Soil microbes Soil invertebrates Herbivores | Climate Soils |
| | Pollination | | Phenology, allocation to reproduction, flower morphology, pollinator specificity | Pollinators | Climate Soils Topography |
| | Soil water availability (see water quantity, above) | | | | |

[a] Adapted from Brauman et al. 2007, Kremen 2005, van der Putten et al. 2004.

[b] Some services are incorporated as "key processes" of others (e.g., erosion control, nutrient cycling). This suite of factors guides us in determining: measurement approaches, predictions based on current data available, and new conceptual frameworks to improve our understanding of services.

groundwater storage and flow. Watershed-level stream flow, which integrates all of the above processes, is the most direct indicator of water supply. A number of studies have shown that vegetation composition strongly affects stream flow (reviewed in Wilcox et al. 2006). However, watershed-level measures of water output through stream flow are not prevalent and could be particularly difficult when assessing the effects of invaders because they would require either long-term preinvasion and postinvasion monitoring or paired invaded and uninvaded watersheds that share all other key characteristics. Many studies have suggested that invaders are likely to decrease water supply, based on invaders having high transpiration rates, compared with natives. For example, measures of leaf transpiration rates have mixed results, suggesting that the invasion of tamarisk into riparian areas of the southwestern United States does not affect or greatly decreases water quantity. However, subsequent studies at larger scales have shown that the invasion of tamarisk often has no measurable effect on water availability because it replaces, rather than increases, stand leaf area, the key driving variable of stand-level transpiration rates (reviewed in Wilcox et al. 2006).

If the process studied is the main driver of an ecosystem service, it will likely be a strong indicator. Yet selecting which processes to use as indicators is not a simple task because ecosystem types differ in which processes are the main contributors to a given service (Feld et al. 2009). For example, it is often assumed that the introduction of woody species will decrease water flow because of higher transpiration rates of woody vs. herbaceous species. In Mediterranean systems, conversion of grasslands to shrublands often decreases water runoff and stream flow because of the higher transpiration rates of the shrubs (Wilcox et al. 2006). However, in arid regions where shrub cover is more discontinuous, shrubs increase water flow by decreasing infiltration of water into the soil, thus increasing overland flow and concentrating flow into deeper, larger channels (reviewed in Eviner and Chapin 2003). Because of different processes dominating provision of water supply, woody encroachment may have dramatically different effects in neighboring regions.

**How Strong Are Our Broad Generalizations about the Effects of Plant Invaders on Ecosystem Processes?** Can we take our measures of invader effects on a given area and extrapolate them across an invader's range? Many assessments of ecosystem services are based on assumptions about the effects of different vegetation types (Bennett et al. 2009; Naidoo et al. 2008). For example, replacement of herbaceous-dominated systems with woody species is often assumed to result in decreased water supply and increased carbon sequestration. Introduction of legumes into an ecosystem are assumed to enhance nitrogen availability. Although all of these assumptions have been supported by

some studies, other studies have shown that the effects of vegetation types or even individual species on ecosystem processes cannot be extrapolated across all system types or even across different patches within a given ecosystem (reviewed in Ehrenfeld 2003).

The previously discussed example of the effects of shrubs vs. grasses on water flow clearly demonstrates that we cannot simply assume woody species will decrease water flow by higher evapotranspiration because the mechanisms by which vegetation can control water quantity vary across ecosystems. This is not only true across different types of ecosystems but also within the same watershed, where woody species may only affect water flow in the presence of deep groundwater that nonwoody vegetation cannot use (Wilcox et al. 2006). As for the assumption that woody species will increase ecosystem stores of carbon and nitrogen, that also cannot be broadly applied across all conditions. Conversion of herbaceous to woody species increases soil C and N at low-precipitation sites ($<300$ mm/yr), but decreases soil C and N as precipitation increases (600 to 1,000 mm/yr). The decreases in soil C and N are of a large enough magnitude that they result in a net ecosystem loss of C and N, even though the woody species do increase C and N sequestered in biomass (Jackson et al. 2002).

Although broad differences in vegetation structure or functional types have long been assumed to have large effects on ecosystem processes, it has only recently been acknowledged that there are some broad generalizations across invasive species. *On average*, invasive plants tend to increase NPP, decomposition rates, and N cycling (Ehrenfeld 2003; Corbin and D'Antonio 2004; Liao et al. 2008). Those patterns are predictable based on the principles that invaders tend to be faster growing, with higher nutrient demands, and such fast-growing, high-nutrient species promote faster nutrient cycling and higher NPP (Chapin 1980). However, there are many exceptions to those overall patterns (reviewed in Ehrenfeld 2003). For example, many rangeland invaders greatly decrease NPP as well as livestock productivity and can slow down nutrient cycling (reviewed in Eviner et al. 2010). When possible, it is far better to predict invader effects based on the functional attributes of the specific invader, compared with natives, rather than just on generalizations about invasives as a whole.

Even when studying a specific invasive species, care must be taken in extrapolating the effects measured in one study to its entire range. For example, downy brome (*Bromus tectorum* L.) increases nitrogen cycling rates in cool deserts but decreases rates in warm, arid grasslands (reviewed in Ehrenfeld 2003). Similarly, spotted knapweed (*Centaurea stoebe* L.) can increase, decrease, or have no effect on soil C and N, depending on the specific site of invasion (reviewed in Eviner et al. 2010). The effect of mouseear hawkweed on soil C and N pools depends on aspect and grazing intensity

(Scott et al. 2001). Kudzu emits isoprene and nitrogen oxides, which together increase levels of tropospheric ozone (Hickman et al. 2010; Sharkey and Loreto 1993). The amount of isoprene emitted by kudzu varies significantly with light intensity, drought stress, and temperature (Sharkey and Loreto 1993). In addition, the contribution of kudzu to air pollution will be more marked in areas that have lower rates of ozone formation (areas far from urban areas, with little or no fertilization) (Hickman et al. 2010).

The prevalence of these context-dependent effects does not suggest that the effects of invasive species are unpredictable, just that we need to improve the assumptions that underlie our predictions. By focusing on mechanisms, rather than simply on patterns, there are clear explanations for many of these context-dependent effects, which can lead to a predictive framework. For example, the effects of a vegetation group or a given species can vary over environmental conditions because of (at least) the following:

(1) Shifts in which mechanisms or plant traits affect a given ecosystem process (e.g., litter chemistry is a key determinant of plant effects on N cycling under mesic conditions but decreases in importance when soil moisture becomes more limiting)

(2) Shifts in key traits of an organism (e.g., root allocation decreases when site fertility increases, thus increasing potential for erosion)

(3) Shifts in the ecosystem effects of a given trait (e.g., labile C inputs can stimulate decomposition of recalcitrant organic matter under low-nutrient conditions but inhibit decomposition of recalcitrant compounds under high-nutrient conditions) (reviewed in Eviner and Hawkes 2008).

Intensifying our measurements of invader effects across space and time will strengthen our ability to account for context-dependence and will also strengthen our extrapolations of local process measures to landscape-scale services.

**Temporal and Spatial Scaling.** How, when, and where do we take measurements for services (or for the processes that serve as indicators) to make large-scale, longer-term assessments? It is extremely challenging to extrapolate short-term, local measures to the longer term and larger scales that are often the focus of ecosystem service assessments. For example, water supply is a regional service that is affected by a number of processes occurring at different scales (Brauman et al. 2007), and measurements at multiple scales can differ in their assessments of the effect of a vegetation type on water supply. For example, based on tree-scale measures, removal of a native tree species was predicted to greatly increase water supply in a Texas watershed. However, those tree-scale transpiration rates extrapolated to the watershed scale suggested that the total amount of water loss through tree transpiration was equivalent to total annual precipitation, an unreasonable estimate (Wilcox et al. 2006). In contrast, measurements of plant water use and supply at the stand (Dugas et al. 1998), catchment (Huang et al. 2006), and landscape levels indicated little to no effect of tree removal on water supply, largely because of compensatory water use by replacement plants (reviewed in Wilcox et al. 2006).

Another challenge in extrapolating plot-based measurements out to larger scales is the prevalence of context-dependent effects. Understanding this variability is critical not only to quantify a service but also to map its location and account for its variability over time (Naidoo et al. 2008). The challenge in sampling for heterogeneity in invader effects is present at the patch to landscape levels. Within a vegetation patch type, measurements must account for local-scale variability in processes associated with native vs. exotic plants. For example, when continuous vegetation cover is replaced by species with clumped distributions, measurements must be taken to incorporate the areas covered by both vegetation and by interspaces. Bare spaces between clumped vegetation can greatly enhance erosion, as seen with the replacement of native grasses by the invasive spotted knapweed (Lacey et al. 1989). Similarly, the assessment of soil C storage in native- vs. exotic-dominated grasslands requires accounting for differences in the depths at which these vegetation types input C (V. Eviner and C. V. Hawkes, unpublished data).

The location of an established population of invasive plant species can affect the delivery of ecosystem services. For example, invasion of woody species into an area with deep groundwater (that only the woody invader can access) will decrease stream flow, but invasion of this same species into other areas of the landscape (without groundwater within reach of the invader's roots or with groundwater in reach of the natives' roots) will lead to little change in stream flow (Wilcox et al. 2006). Where a vegetation type is located across the landscape is also critical because certain ecosystem processes and services are largely concentrated in "hot spots" across the landscape (McClain et al. 2003). For example, filtration of nutrients and soil particles relies on wetlands or vegetation buffer strips lying within the flow path of areas from which nutrients and soil are being lost. The size of a vegetation patch type also has significant effects on ecosystem services, so that ecosystem services may depend on the extent of invasion. The area of land needed to reliably provide a service is generally unknown (Kremen 2005), although some guidelines are available for water quality. On average, 20% of the catchment upland vegetation must be converted to see effects of land cover change on water flow at the watershed level, although these effects can be observed with as little as 15% conversion or not until at least 50% of land cover has changed (reviewed in Brauman et al. 2007). A watershed requires an estimated 2 to 7% cover of wetlands to improve water quality

(Verhoeven et al. 2006). Similarly, in the Mississippi River basin, 1 to 2% cover of small-stream riparian zones and wetlands are estimated to remove 20 to 50% of the N from the river (Mitsch et al. 2001).

To assess the ecosystem effects of an invasive species, not only the spatial extent of the invasion but also the density of invasion within a given patch are important. Historically, it has been assumed that the effect of an invader is proportional to its abundance, implying that invaders would only affect ecosystems if they dominated patches (Grime 1998). However, recent work indicates that some plants can have large effects on ecosystem processes even at very low abundances (< 3 to 5% of plant cover or biomass) (Elgersma and Ehrenfeld, 2011; Marsh et al. 2000; Peltzer et al. 2009). For example, in a river floodplain in New Zealand, nonnative plants made up < 3% of plant community biomass but had significant effects on soil C, microbial biomass, and microbial community structure (Peltzer et al., 2009).

The abundance and extent of an invader can change over time, and its ecosystem effects can also accumulate with time since invasion. For example, alteration of soil organic matter and the subsequent effects of that on C storage, water infiltration, and nutrient cycling and storage are likely to increase with time since invader establishment (reviewed in Strayer et al. 2006). The integration of functional dissimilarity, abundance, extent, and time since invasion can be used to predict which invaders are likely to affect ecosystem processes. This same framework can be extended to assess invader effects on ecosystem services, with careful attention to how individual processes relate to services and scaling of invader effects on processes over space and time, as discussed below.

Just as spatial scales must be specifically considered, temporal scales are also critical. Similar to hot spots across the landscape providing key services, hot moments can govern the provision of ecosystem services (McClain et al. 2003). For many hydrologic services, such as flood prevention, average precipitation events are irrelevant, and ecosystem processes during large, infrequent storms are the key determinants of services (Bennett et al. 2009). Seasonality in invader activity (phenology) compared with natives can have large effects on ecosystems. For example, the invasion of broomsedge (*Andropogon virginicus* L.) into Hawaiian woodlands has resulted in the creation of boggy conditions because maximum evapotranspiration of the invader did not coincide with the rainy season (Mueller-Dombois 1973). Similarly, invasion of exotic grasses into California grasslands greatly increases the volume of water leached from the soil early in the season (V. Eviner and C. V. Hawkes, unpublished data), when the system is most susceptible to nitrogen leaching loss (Lewis et al. 2006). Similarly, in British Columbia estuaries, the rapid decay of purple loosestrife (*Lythrum salicaria* L.) compared with native sedges was found to supply detritus in the fall season, creating a resource pulse that may disrupt food webs of native, juvenile salmon that are adapted to take advantage of detritus provided in the winter and spring (Grout et al. 1997).

Variability in the effects of the invader over time can also be critical to consider. Primary productivity may vary more with interannual variability of precipitation than with vegetation shifts (Fuhlendorf et al. 2009), or the variability can be greater with a certain land cover type. For example, net primary production of systems invaded by downy brome can vary 10-fold on an annual basis, greatly affecting the reliability of forage production (Hull and Pechanee 1949).

It is also critical to consider the long-term effects of invasive species. Some effects will only be seen after the invader has been present for decades to centuries (reviewed in Strayer et al. 2006). For example, in dune systems, Sydney golden wattle [*Acacia longifolia* (Andr.) Willd.] alters nitrification rates and litter accumulation within the first decade of invasion, but nutrient sequestration is only altered after more than 20 yr (Marchante et al. 2008). In such cases, the best indicator of soil fertility may change over time.

## Improving the Assessments of Invasive Plant Effects on Ecosystem Services

Current ecosystem service assessments are often based on assumptions about the services delivered by a certain land cover type or by using measures of ecosystem processes that are one of a number of processes that collectively provide the service. Although these proxies for services are rough, they are a solid foundation for current assessments. Our review suggests that existing approaches will greatly improve by (1) determining which processes are the key contributors to a service and how those processes change with environmental conditions, (2) assessing how multiple processes interact to provide a given service, (3) determining how vegetation types and species affect services, and (4) explicitly assessing how ecosystem services and their controls vary over space and time, including reliance of ecosystem services on hot spots and hot moments and the minimum size of a vegetation type in the landscape (Figure 1). Many of these components are already well understood for individual ecosystems (Table 1), and although there are still significant gaps in our understanding of how these components interact to drive ecosystem services (Kremen 2005), this approach will be an improvement over our current crude assessments (Bennett et al. 2009; Naidoo et al. 2008) and can fill a great need in ecosystem management to assess promising management practices for controlling invasive species and their effects on ecosystem services (Briske 2011).

It is critical to consider the trade-offs, synergies, and interactions across multiple services. Most services are not

tightly correlated with one another in their distribution across the landscape (e.g., Bennett et al. 2009; Egoh et al. 2008), and plant species have independent effects on multiple processes (Eviner and Chapin 2003), so how we manage for a balance of services may need to shift across the landscape. This is particularly important because management for any one service (e.g., crop production, C sequestration, water supply) can sometimes enhance other services but often greatly compromises the provision of other services and even the resilience of a system (Bennett et al. 2009; Gordon 1998, Millennium Assessment 2004). The spread of invasive species and our management of those invaders can strongly affect multiple services. In the case of long-term invaders, in particular, we must carefully assess the multiple roles that the invader is playing before we try to remove it. Invaders can become so integrated in ecosystem and community dynamics that their removal disrupts ecological processes, such as food web interactions (reviewed in Zavaleta et al. 2001).

We must also consider that invasions of exotic species may be symptoms of shifting environmental conditions that will no longer support the native community, a concept known as *novel ecosystems* (Hobbs et al. 2009). In the case of novel systems, invasive species may not be disrupting ecological processes but may be sustaining or restoring ecosystem services under a shifting environment (Hobbs et al. 2009). Although plant invasions clearly can have strong negative effects on native plant communities (Vila et al. 2010), it should not be assumed that their effects on ecosystem services will always be detrimental. Effective management of ecosystem services will require a better understanding of the thresholds at which those invasive plants are critical for ecosystem resilience.

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