

Introduced and Invasive Species in Novel Rangeland Ecosystems: Friends or Foes?

Jayne Belnap,¹ John A. Ludwig,² Bradford P. Wilcox,³ Julio L. Betancourt,⁴ W. Richard J. Dean,⁵ Benjamin D. Hoffmann,⁶ and Sue J. Milton⁷

Authors are ¹Research Ecologist, US Geological Survey, Moab, UT 84532, USA; ²Honorary Fellow, CSIRO Ecosystem Sciences, Atherton, QLD 4883, Australia; ³Professor, Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843, USA; ⁴Research Scientist, US Geological Survey, Tucson, AZ 85719, USA; ⁵Research Associate and ⁷Honorary Professor, DST/NRF Centre of Excellence, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa; and ⁶Senior Research Scientist, CSIRO Ecosystem Sciences, Winnellie, NT 0822, Australia.

Abstract

Globally, new combinations of introduced and native plant and animal species have changed rangelands into novel ecosystems. Whereas many rangeland stakeholders (people who use or have an interest in rangelands) view intentional species introductions to improve forage and control erosion as beneficial, others focus on unintended costs, such as increased fire risk, loss of rangeland biodiversity, and threats to conservation efforts, specifically in nature reserves and parks. These conflicting views challenge all rangeland stakeholders, especially those making decisions on how best to manage novel ecosystems. To formulate a conceptual framework for decision making, we examined a wide range of novel ecosystems, created by intentional and unintentional introductions of nonnative species and land-use-facilitated spread of native ones. This framework simply divides decision making into two types: 1) straightforward-certain, and 2) complex-uncertain. We argue that management decisions to retain novel ecosystems are certain when goods and services provided by the system far outweigh the costs of restoration, for example in the case of intensively managed *Cenchrus* pastures. Decisions to return novel ecosystems to natural systems are also certain when the value of the system is low and restoration is easy and inexpensive as in the case of biocontrol of *Opuntia* infestations. In contrast, decisions whether to retain or restore novel ecosystems become complex and uncertain in cases where benefits are low and costs of control are high as, for example, in the case of stopping the expansion of *Prosopis* and *Juniperus* into semiarid rangelands. Decisions to retain or restore novel ecosystems are also complex and uncertain when, for example, nonnative *Eucalyptus* trees expand along natural streams, negatively affecting biodiversity, but also providing timber and honey. When decision making is complex and uncertain, we suggest that rangeland managers utilize cost-benefit analyses and hold stakeholder workshops to resolve conflicts.

Resumen

Mundialmente, nuevas combinaciones de plantas introducidas e inducidas y especies de animales han cambiado los pastizales a nuevos ecosistemas. Mientras que muchos de los interesados en los pastizales (personas que usan o tienen interés en los pastizales) ven un beneficio en la introducción de especies para el mejoramiento de la producción de forraje y control de la erosión, otros se interesan en los costos no planeados tales como el aumento en el riesgo de fuego, pérdida de biodiversidad en los pastizales y amenazas en los esfuerzos de conservación especialmente en reservas naturales y parques. Estos puntos de vista conflictivos son retos para todos los interesados en los pastizales, especialmente para la toma de decisiones en cómo manejar mejor los ecosistemas nuevos. Para formular un modelo conceptual para toma de decisiones, examinamos un amplio rango de ecosistemas nuevos, creados de manera intencional y no intencional de especies no nativas y el uso de tierras que facilitan la expansión de especies nativas. Este modelo simplemente divide la toma de decisiones en dos tipos: 1) francamente-seguro y 2) complejo-no seguro. Discutimos que las decisiones de manejo para mantener ecosistemas nuevos son seguras cuando los bienes y servicios proporcionados por el sistema sobrepasan por mucho el costo de restauración, por ejemplo en el caso de las praderas intensivas de *Cenchrus*. Las decisiones para devolver ecosistemas nuevos a sistemas naturales son también seguras cuando el valor del sistema es bajo y la restauración es fácil y barata como en el caso del control biológico de las infestaciones de *Opuntia*. En contraste, las decisiones ya sea de mantener o recuperar ecosistemas nuevos se complican y son inciertas en casos donde los beneficios son bajos y los costos altos, por ejemplo en el caso de detener la expansión del *Prosopis* y *Juniperus* en los pastizales semiáridos. También las decisiones para mantener o renovar un ecosistema nuevo son difíciles e inciertas cuando por ejemplo, especies no nativas como el Eucalipto se extienden sobre arroyos naturales afectando negativamente la biodiversidad pero también proveyendo madera y miel. Cuando el proceso de toma de decisiones es complejo e incierto sugerimos que los manejadores de pastizales usen el análisis de costo beneficio y talleres entre los interesados para resolver conflictos.

Key Words: *Cenchrus*, decision framework, *Eucalyptus*, *Juniperus*, *Opuntia*, *Prosopis*, rinderpest, West Nile virus

INTRODUCTION

Most rangelands around the world are at least partially dominated by “novel” or “emerging” ecosystems, that is, those containing new combinations of plants and animals arising as a result of direct or indirect human influence (Hobbs et al. 2006; Bridgewater et al. 2011). In rangelands, these novel systems

Research was funded by the US Geological Survey, Ecosystems Program (Belnap), USDA–National Institute of Food and Agriculture (NIFA) Managed Ecosystem Award 2010-85101-20485 and NIFA/NRCS Award 2008-51130-19562 (Wilcox), and Rufford Small Grants Foundation, United Kingdom (Dean, Milton).

Correspondence: Jayne Belnap, Research Ecologist, US Geological Survey, 2290 South Resources Blvd, Moab, UT 84532, USA. Email: jayne_belnap@usgs.gov

Manuscript received 26 August 2011; manuscript accepted 6 May 2012.

generally result from management-induced changes in native plant communities, which create opportunities for invasions or increases in the density (or the range) of alien or native species (Milton et al. 2007). Some of these species can be managed through their removal or containment, whereas other species appear uncontrollable.

Many species have been intentionally introduced to rangelands for purposes beneficial to humans (e.g., erosion control, shade, forage). Purposeful introductions may continue to be of value in some circumstances, whereas in others the introduced species may have produced unintended and detrimental consequences and a case can be made for their removal. The likelihood of novel ecosystems appearing in rangelands will only increase with time because of globalization, climate change (and novel climates), nitrogen deposition, and land-use intensification. The prescriptions for managing these novel ecosystems will be increasingly nuanced, calling for control of some species and not others, and in some places and not others. Who will make these decisions, and on what basis, at what expense, and over what time frame?

Proactive land management is becoming increasingly difficult as past mistakes and current crises consume the time and resources of land managers (Hobbs et al. 2003; Seastedt et al. 2008). Even more difficult is establishing targets for restoration or predicting the future “look” for ecosystems. Past analogs may become increasingly irrelevant because the current range of biotic and abiotic conditions controlling the structure and function of a given ecosystem may be substantially altered, and the influence of these future conditions remains unknown (Fox 2007; Seastedt et al. 2008). In addition, interglacial periods like the Holocene (the last 13,000 yr) characterize only 10 percent of the last million years and are hardly the norm, and in many parts of the world modern biotic communities are only thousands of years old in both composition and distribution (Lyford et al. 2003). The future promises to be even more fleeting as both native and nonnative species, some fast and others slow-moving, shift their distributions across highly human-altered landscapes in response to a continuously and rapidly changing climate.

In many cases, we may no longer be able to constrain many systems within past or even current abiotic or biotic boundaries, but will need instead to learn to accept the new conditions and ecosystems that can exist within these new boundaries (Hobbs et al. 2006). In other cases, current or recently altered ecosystems may be of such high societal value that extraordinary efforts will be made to keep them viable. Facing the challenge of managing novel ecosystems will require transformational, rather than incremental, approaches to land management. These challenges will compel land managers to be even more forward thinking and to adopt new methodologies (Holling 2001).

In this paper, we briefly discuss examples of novel ecosystems created by species that occur on at least two of three continents (Africa, Australia, and North America). These ecosystems were formed by 1) intentionally introducing invasive plants (*Cenchrus* [*Pennisetum*], *Eucalyptus*, *Opuntia*); 2) unintentionally introducing animals (fire ants) and viral diseases (West Nile virus, rinderpest); or 3) unintentionally, through land use, increasing the density of native woody plants (*Juniperus*, *Prosopis*). We discuss how these organisms have altered the

communities in which they occur to form novel ecosystems and how managing these systems depend on site-specific goals. We then provide a simple conceptual framework to assist land managers in making decisions about how to respond to novel ecosystems.

CASE STUDIES

Grasses and Succulents

***Cenchrus ciliaris* (L.)**. Native to Africa, the Middle East, across to India, and Indonesia, *Cenchrus ciliaris* (syn. *Pennisetum ciliarum*) (buffel grass) now occurs in many countries around the globe (Marshall et al. 2011). In some rangelands, such as in areas of central and northern Australia, and in northern Mexico and the southwestern United States, *C. ciliaris* can be an aggressive invader and has formed novel ecosystems.

In Australia, *C. ciliaris* was introduced intentionally in the 1870s by Afghan cameleers who discarded *C. ciliaris* when restuffing worn saddle packs and harnesses brought from their homelands (Winkworth 2000). To improve grazing and drought-affected rangelands, *C. ciliaris* was also intentionally introduced to Australia beginning in the late 1950s, and has become a mixed blessing (Friedel et al. 2006). To cattle producers, *C. ciliaris* is very desirable because it establishes highly productive, self-sustaining stands on a wide variety of soil types, especially in tropical and subtropical areas dominated by summer rainfall (Fig. 1). In such environments, *C. ciliaris* can replace native grasses, particularly when landscapes are grazed or disturbed by flooding and fire. Frequent and hot fires can favor *C. ciliaris* (Miller et al. 2010). It is also of value for rehabilitating eroded rangelands and disturbed mine sites, as it provides excellent ground cover.

Whereas these characteristics make *C. ciliaris* a friend to some land managers, its biological and ecological attributes make it a foe to those aiming to conserve natural ecosystems (Friedel et al. 2006). With disturbance, *C. ciliaris* invades natural grasslands and savannas, altering landscape processes



Figure 1. Brahman cattle grazing a *Cenchrus ciliaris* pasture in the Upper Burdekin Catchment, Queensland, Australia, a region with relatively consistent and abundant summer rainfall. (Photo: J. A. Ludwig.)

such as runoff, erosion, and biodiversity (Ludwig and Tongway 2002; Smyth et al. 2009).

Given that *C. ciliaris* is in Australia to stay, and can be a friend or foe to people living in the same landscape, strategic plans are being developed to achieve both production and conservation goals (Friedel et al. 2006). These plans require resolution of conflicts, trade-offs, and compromises. They also highlight further research needs on how to reduce the negative impacts of *C. ciliaris* (e.g., using grazing to reduce fire risk around settlements, and maintaining forage while minimizing impacts on biodiversity).

To improve cattle forage, *C. ciliaris* has been planted in pastures in North, Central, and South America, and even Hawaii, where it has escaped into nonpastures. Whereas it is deemed a “wonder grass” by cattle ranchers in south Texas (United States) (Hanselka 1988) and northern Mexico (Arriaga et al. 2004), *C. ciliaris* is considered a scourge by conservationists and wildlife managers throughout the southwestern United States (Burquez-Montijo et al. 2002), and is officially listed as a noxious weed in southern Arizona (United States) (Halvorson and Guertin 2003). In the Sonoran Desert, straddling northern Mexico and southern Arizona, *C. ciliaris* is rapidly transforming Sonoran Desert shrublands, containing columnar cacti and rare plants, into impoverished grasslands by both increasing fire risks where wildfires were historically small and infrequent (Burquez-Montijo et al. 2002) and outcompeting native plants (Olsson et al. 2012). Not only rare species, but also more dominant and iconic ones like the saguaro (*Carnegiea gigantea*) are at risk from this invasive grass species. Impacts to basic ecosystem services, including food webs, nutrient cycling, and hydrologic cycles, remain unstudied, but are likely to be substantial. Economic impacts include market-based costs (e.g., decreased property values in fire-prone areas, losses in tourism revenues with a decaying ecological backdrop, and escalating weed control and fire suppression budgets) as well as non-market-based costs not easily expressed in dollar terms (i.e., aesthetic values).

In Tucson, Arizona, and surrounding areas, both the public and private sectors have coordinated their efforts to control the further spread of *C. ciliaris*. For example, federal land management agencies and local governments are collaborating in an experiment to evaluate collateral damage to native plants by precision herbicide spraying of *C. ciliaris* from a helicopter (Holcombe et al. 2012). Data management systems and vulnerability and risk assessments are being integrated into a state-and-transition, decision analysis framework parameterized for habitat suitability, invasion rates, dispersal dynamics, and treatment costs and effectiveness (Frid et al. 2012). The control effort in southern Arizona, a wealthy region also rich in science and conservation, is exemplary; if it fails there, it may not be feasible anywhere else.

***Cenchrus setaceus* (Forssk.) Marrone.** Also an invader, *C. setaceus* (syn. *Pennisetum setaceum*) originates from North Africa and the Middle East (Williams et al. 1994). Commonly known as fountain grass, it is now found in rangelands of Australia, Hawaii, Namibia, North America, and South Africa. In South Africa, *C. setaceum* frequently occurs alongside *C. ciliaris* (Rahlao 2009). *Cenchrus setaceum* has pink inflorescences and drought hardiness, which makes it attractive for

low-maintenance gardens, and its extensive fibrous root system makes it useful in rehabilitation projects (Halvorson and Guertin 2003). Dense stands of *C. setaceum* increase fire frequencies, which reduces native plants and available forage (D’Antonio and Vitousek 1992; D’Antonio et al. 2000; Rahlao et al. 2009). Efforts are underway to eradicate this plant in native ecosystems where possible.

***Opuntia ficus-indica* (L.) P. Mill.** In 1656, Indian fig opuntia, *O. ficus-indica*, native to the southern United States, was introduced into South Africa as a drought fodder (Annecke and Moran 1978; Wells et al. 1986) (Fig. 2). Although the selected spineless form of this species had been introduced, most plants originating from seeds and spread by birds and primates developed spines. In the late 1800s, the range of *O. ficus-indica* in South Africa began expanding (Zimmerman and Moran 1991), and by 1942 this cactus covered 900,000 ha of rangelands, reducing the yield and accessibility of grass for cattle and small stock (du Toit 1942). Biocontrol by the introduced cochineal beetle, *Dactylopius opuntiae*, markedly reduced *O. ficus-indica* density by 1948 (Zimmerman et al. 1986), and has kept populations low and localized, despite dispersal by humans, monkeys, baboons, elephants, tortoises, and birds that deposit seeds in protected establishment sites among boulders and below trees (Dean and Milton 2000). In



Figure 2. *Opuntia ficus-indica* at the base of a transmission pole (probably dispersed to the site by crows), Aberdeen, Eastern Cape, South Africa. (Photo: S. J. Milton.)

addition to *O. ficus-indica*, at least 13 other species of invasive cacti have been introduced into southern Africa by the horticultural industry and have spread into natural rangelands (Henderson 2001).

***Opuntia stricta* (Haw.) Haw.** The common prickly pear cactus, *O. stricta*, native to the Caribbean, was planted in Australia as an ornamental and along fence rows in the late 1800s, and by the 1920s had invaded extensive rangeland areas, especially in northern New South Wales and central Queensland (Parsons and Cuthbertson 2001). It has also invaded parts of South Africa (Foxcroft and Rejmánek 2009). Most *Opuntia* invasions have been effectively controlled by the beetle, *Dactylopius opuntiae*, native to the United States and Mexico, and by the moth, *Cactoblastis cactorum*, native to Argentina, Brazil, Paraguay, and Uruguay (Zimmerman et al. 1986). Ironically, *C. cactorum* was also introduced to countries in the Caribbean and now poses a serious threat to the rich cactus flora indigenous to the United States and Mexico (Zimmerman et al. 2001).

Woody Plants

One of the most significant global transformations of rangelands is the increasing abundance of both native and nonnative woody plants (Eldridge et al. 2011). This transformation is driven by a history of overgrazing, changes in fire regimes, increasing CO₂, and global warming (Archer et al. 2001).

***Prosopis* spp.** On the North American continent, the native shrub genus *Prosopis*, especially the species *Prosopis glandulosa* Torr. (honey mesquite) and *Prosopis velutina* Woot. is increasing in northern Mexico and the southwestern United States. Together, these two species cover more than 30 million ha (Bovey 2001). *Prosopis* was historically most common in certain parts of the landscape, such as drainages or river courses. The expansion of *Prosopis* into grasslands of the United States has been phased and related to patterns of settlement. In the Rio Grande Plains of southern Texas, United States, the conversion from grassland to shrubland began in the 1800s (Bogusch 1952). The Rio Grande Plain is now mostly a subtropical thorn woodland with *P. glandulosa*, honey mesquite, being one of the dominants (McLendon 1991). In the southern high plains and the southwest United States, the conversion began around the beginning of the last century, following the historical overgrazing that occurred in the region from around 1880 to 1900 (Box 1967; Hennessy et al. 1983). In terms of aerial coverage, the expansion of *Prosopis* woodlands was largely complete by the 1960s (Bovey 2001), although the density of these woodlands continues to increase up to the present day (Archer et al. 2001).

In Australia, species of *Prosopis* were introduced from North America (e.g., *P. glandulosa*, *P. velutina*) and South America (e.g., *Prosopis pallida*) in the early 1900s (van Klinken and Campbell 2001). They were planted as shade trees around homesteads and in towns, and in paddocks to provide livestock shelter and a food source, but *Prosopis* species have now encroached into productive rangelands to form shrublands with very low forage value for livestock. Many *Prosopis* produce fruits (long pods) that are sweet and beans that are high in protein. Livestock (e.g., cattle, horses), feral pigs, and native animals (e.g., kangaroos, emus) relish *Prosopis* fruits and thus efficiently spread undigested beans,

which readily germinate to establish new plants. *Prosopis* fruits are also spread by floods, so that the tree is becoming increasingly abundant along many watercourses.

Because *Prosopis* seeds planted in Australia were sourced from different species and environments, *Prosopis* has demonstrated the potential to thrive in a wide range of climates and soils and in some locations, have hybridized (van Klinken and Campbell 2001). In Australia, *Prosopis* is currently only a major threat in localized areas where it affects livestock grazing and biodiversity. In 2011, *Prosopis* ranked second of 20 declared Australian “Weeds of National Significance”¹ because of its current widespread but localized distribution across rangelands, potential to spread further, and high environmental and economic impacts.

Similarly in South Africa, nonnative *P. glandulosa*, *Prosopis juliflora*, and *P. velutina* and their hybrids are problem invasives (Richardson et al. 2000). *Prosopis* trees have value to farming communities because they provide timber, fuel, shade, forage and shelter for livestock, and nectar for honeybees, and they fix atmospheric nitrogen, stabilize dunes, control runoff and colonize bare areas. However, dense stands of *Prosopis* reduce water availability to wildlife in ephemeral watercourses and water supplies for agriculture and human settlements (Richardson et al. 2000). Therefore, *Prosopis* is one of the targets of the South African national Working for Water poverty relief program (Fig. 3) (Koenig 2009). Furthermore, *Prosopis* trees can form dense thickets that are almost impenetrable to game and cattle (Harding and Bate, 1991). Even in more open thickets where herbivores can utilize *Prosopis* plants, and their pods, some dung beetle species (*Scarabeidae*) cannot navigate between the plants, resulting in reduced dung beetle species richness and amount of dung recycled (Steenkamp and Chown 1996).

Birds are also affected when *Prosopis* forms dense monospecific stands, leading to lower bird diversity and a disruption of bird-mediated ecosystem processes. Bird and plant diversities



Figure 3. *Prosopis* thicket being cleared by the Working-for-Water Programme, near Britstown, Northern Cape, South Africa. (Photo: S. J. Milton.)

¹<http://www.weeds.org.au/WoNS/>

were found to be lower in *Prosopis*-dominated woodlands than in native *Acacia* woodlands (Dean et al. 2002). In woodlands, lower bird diversity reduces seed rain of fleshy-fruited plant species, with resulting negative feedbacks to the vegetation (Milton et al. 2007).

***Juniperus* spp.** A number of *Juniperus* species are expanding in North American rangelands to form novel woodlands (Fig. 4). In general, the increase in these woodlands has been related to a decline in the frequency of fires, excessive grazing (Burkhardt and Tisdale 1976) and, more recently, to other factors such as landscape fragmentation, elevated CO₂, global warming, and large precipitation events (Knapp et al. 2001; Briggs et al. 2005). However, in Wyoming (United States), the recent spread and infilling by *Juniperus osteosperma* (Torr.) Little may be a continuation of late Holocene migration, perhaps accelerated by livestock grazing and fire suppression (Lyford et al. 2003).

In the United States, the regions that have seen the most significant expansion of *Juniperus* woodlands include 1) the Edwards Plateau and Rolling Plains of central Texas with *Juniperus ashii* J. Buchholz (Ashe juniper) and *Juniperus pinchotii* Sudw. (redberry juniper) (Ueckert et al. 2001; Diamond and True 2008); 2) the Colorado Plateau and Great Basin, where *Juniperus monosperma* (Engelm.) Sarg. (one-seed juniper) and *J. osteosperma* (Utah juniper) are common (Jacobs et al. 2008); 3) the Columbia Plateau, where *Juniperus occidentalis* Hook. (western juniper) is the dominant species (Miller and Rose 1999); and 4) the Great Plains, where *Juniperus virginiana* L. (eastern red cedar) has been spreading (Scharenbroch et al. 2010). Because of the vast expanse of land affected, the conversion of grasslands to juniper-dominated woodlands represents an enormous ecological and economic change.

As with the *Prosopis* expansion, *Juniperus* woodlands have spread in a phased process. For example, in the rangelands of Texas and the southwestern United States, the process of *Juniperus* expansion began around the turn of the last century, and may now be largely complete (Johnson and Elson 1979; Diamond and True 2008). Depending on how these *Juniperus*



Figure 4. *Juniperus* encroaching into grasslands, Texas, United States. (Photo: B. Wilcox.)

woodlands are managed, however, they may continue to increase in density (Ueckert et al. 2001; Archer et al. 2011). In the northwestern United States, *Juniperus* is continuing to expand (Coppedge et al. 2001), but the area already converted to woodland is large (Miller et al. 2005) and it is uncertain how much additional area may be affected. In the Great Plains the story is quite different because *Juniperus* woodlands are expanding very rapidly, and this process may only be in its early stages. The spread of *Juniperus* in the eastern Great Plains may threaten the survival of remnant tall grass prairies (Briggs et al. 2005).

The response of land managers to the expansion of *Juniperus* has changed. On the basis of economics alone, control measures using expensive mechanical and chemical treatments can rarely be justified. In addition, changes in demographics and land-use perceptions have (in general, although not universally) translated to declining motivation on the part of landowners to manage *Juniperus*-dominated landscapes actively. In some instances, conversion has been so complete that restoration cannot be achieved without radical intervention. Thus, in many cases, society has chosen to live with these altered landscapes and it is difficult to argue that major investments should be made to restore them. However, where small remnants of native communities remain, such as remnant tall grass prairies in the Great Plains, society may decide it is worth investing substantial efforts in restoring or preserving these areas.

***Eucalyptus* spp.** Widely cultivated in South Africa, *Eucalyptus* species (gum trees), native to Australia, are used for timber and honey production (Immelman et al. 1973). Most *Eucalyptus* species in South Africa have been largely noninvasive until recently, when major flooding events allowed for the expansion of *Eucalyptus camaldulensis* Dehnh. (red river gum) into areas with shallow water tables and along small streams (Henderson 2001). These trees are profligate water users, drying out small creeks and reducing river flow (Le Maitre et al. 2002). Their litter fall and shading reduce aquatic life such as dragonflies, damselflies, and frogs (Samways et al. 2011). But *Eucalyptus* trees can offer higher perching and more nesting sites than native trees for small, bird-hunting raptors (Ewbank 2000), impacting on local populations of smaller birds (Hockey et al. 2005). In California (United States), *Eucalyptus* sp. were first planted during the gold rush, but they have since been widely planted in the western United States and southwestern Canada for timber, shade, and other purposes. In some areas *Eucalyptus* are invasive, creating fire hazards and other problem (Santos 1997).

Viral Diseases

***Morbillivirus* sp. (Rinderpest).** In the late 1800s and early 1900s, rinderpest (cattle plague), an infectious viral disease from Asia, swept through the African continent, causing rapid mass mortality of cattle and other split-hooved ungulates, with subsequent losses of top predators that relied on these ungulates as prey (Stevenson-Hamilton 1957). As in other parts of Africa, rinderpest markedly affected populations of certain species of ungulates in the Kruger National Park region in South Africa, whereas other ungulate species populations were less affected (Rossiter 1994). This subsequently changed the ratios of selective

feeders to rather more nonselective feeders and bulk grazers. It is thought that this shift in feeding patterns may have increased grass biomass and accumulated fuel load, resulting in more frequent, and more intense fires, and consequently more open savanna habitats (Bengis et al. 2003).

The depopulation of wildlife in southern Africa through rinderpest occurred at the same time human populations, who depended on wild game for meat, were rapidly increasing (Talbot 1961). Combined with fencing of properties, overgrazing by livestock, and predator control, these factors disrupted ecological processes and restructured ecosystems at an unprecedented rate and scale, leaving most African rangelands as novel ecosystems.

Flavivirus sp. (West Nile Virus). Another insidious viral disease is West Nile virus, thought to be carried by mosquitoes. It has spread rapidly across North America, has reached Central America and the Caribbean, and could potentially reach South America and Hawaii (Marra et al. 2004). *Flavivirus* sp. impacts populations of humans and other mammals, birds, and reptiles, but little is known about how it affects ecosystems. However, it appears to impact some species more than others, and thus has the potential to affect ecosystem patterns and processes. There are few actions possible to protect wild animal populations, other than general mosquito control. However, because of costs, effective controls are only possible in limited geographical areas.

Invasive Ants

Ants are highly successful invaders globally (Williams 1994; Holway et al. 2002), and several exotic species cause significant ecological impacts (O'Dowd et al. 2003; Hoffmann and Parr 2008). Outside of their native distributions, most exotic ant species occur within urban areas (Suarez et al. 2001). Most rangelands have not experienced exotic ant invasions, but when they do, most effects are benign, as they merely utilize vacant niches and add to species richness. However, there are two important exceptions: the introduction of *Solenopsis* spp. (fire ants) to the southern United States and *Anoplolepis gracilipes* (yellow crazy ant) to northern Australia.

Solenopsis Spp. (Fire Ants). Since *Solenopsis* spp. (predominantly the red imported fire ant, *Solenopsis invicta* Buren) were accidentally introduced from South America into the southeastern United States in the late 1930s, they have dispersed almost unabated across the southern United States, and have now reached the semiarid rangelands of Texas, Oklahoma, New Mexico, and Arizona. Modeling has shown that approximately the southern half of the United States is suitable habitat for *S. invicta* (Korzukhin et al. 2001; Morrison et al. 2004), and without successful intervention most southern rangelands will eventually be inhabited by this species.

Where *S. invicta* invades, its ecological impacts are consistent: notably, dramatic reductions in other invertebrates (Porter and Savignano 1990). However, the severity of its impact is dependent upon the ant's social form and impacts also diminish as rangeland aridity increases and winter temperatures decrease (Camilo and Philips 1994). A few years after *S. invicta* invades, its impacts tend to stabilize so that most invertebrate species that were present preinvasion return, albeit at reduced abundances (Morrison 2002). Some native ant

species appear to persist by shifting their foraging activity times to reduce their interactions with *S. invicta* (Jusino-Atresino and Phillips 1994), which creates novel ant community dynamics.

Reptiles, mammals, and ground-nesting birds are also negatively affected by *S. invicta*, primarily through predation on eggs and young. For example, this species has reduced the survival of waterbird hatchlings by 92% in Texas (Drees 1994). More broadly, *S. invicta* damages infrastructure in urban and rural areas, particularly electric equipment. It is especially notorious as a social hazard, as it has a powerful sting that can induce anaphylactic shock in humans (Solley et al. 2002). In rangelands, livestock (most commonly cattle) are also affected by *S. invicta* stings, often resulting in blindness or death in the livestock and thus human economic loss (Lofgren and Adams 1982).

Attempts to control *S. invicta* with the use of broad-scale treatments of organochlorides have not achieved long-term control, and this method has attained the unenviable global reputation of having one of the greatest nontarget impacts of all management efforts against invasive species (Summerlin et al. 1977). Using chemical control remains feasible in rangelands at a local scale, but to achieve broad-scale control of *Solenopsis* spp., other control methods will be required. One option may be a relatively new biocontrol option with phorid flies (LeBrun et al. 2008). However, many biocontrol efforts have had unintended consequences for native ecosystems and must be approached with caution (Hultine et al. 2010).

Yellow Crazy Ant (*Anoplolepis gracilipes*). Within northern Australia's tropical rangelands, *A. gracilipes* Smith (Fig. 5) has a markedly negative impact on native ant communities, reducing ant species richness by approximately 30% (Hoffmann and Saul 2010). Interestingly, *A. gracilipes* is a large species, and its effect on native ants appears to be restricted to those of approximately equivalent size or larger so that the resultant ant community is almost entirely of small species. Although *A. gracilipes* is better at removing herbivorous insects from foliage than native ant species, this does not necessarily result in better plant protection, with foliage damage being greater where *A. gracilipes* is present (Lach and Hoffmann 2011). Its level of predation on insects is also dependent upon whether the host plant provides a food resource (such as sugar from extrafloral nectaries) or not.

Complete eradication of *A. gracilipes* from Australia is no longer feasible, but recent management efforts to contain it within a single region have been highly successful (Hoffmann 2010). Should this containment effort fail, this invasive ant will eventually impact on ecosystems throughout Australia's northern rangelands.

MANAGING NOVEL ECOSYSTEMS: A FRAMEWORK

Ecosystem services are defined as "the benefits people obtain from ecosystems" (Millennium Ecosystem Assessment 2005), and include *provisioning* services such as food and water; *regulating* services such as regulation of floods, drought, land degradation, and disease; *supporting* services such as soil formation and nutrient cycling; and *cultural* services such as recreational, spiritual, religious, and other nonmaterial benefits (Fig. 6a).



Figure 5. A yellow crazy ant (*Anoplolepis gracilipes*) queen. (Photo: B. Hoffmann.)

Novel ecosystems, like natural systems, can provide supporting and regulating services, as well cultural and provisional goods and services to humans (Chapin et al. 2006). How well novel and natural ecosystems provide these goods and services depends on a number of external socioeconomic and biophysical drivers (Fig. 6a). In many instances, decisions made about the management of novel ecosystems consider the socioeconomic value of novel cultural and provisional services of greater importance than the regulating and supporting services, although this can clearly be shortsighted. However, both scientists and decision makers often lack a basic understanding of novel ecosystem processes (e.g., how external factors affect regulating and supporting services and subsequent impacts on cultural and provisional services). Thus, many decisions need to be made with little or no understanding of the long-term consequences of manipulating novel ecosystems.

We propose a simple framework where the management decisions being made by stakeholders regarding novel ecosystems are of two general types: 1) straightforward-certain or 2) complex-uncertain (Fig. 6b), which are related to a stakeholder-defined matrix of benefits (value of services from the novel ecosystem) versus costs (difficulty of restoring the novel ecosystem to a self-maintaining natural ecosystem). An example of a straightforward-certain situation where the novel ecosystem would be retained (Fig. 6b, cell 2) is when an intentionally created novel ecosystem is providing valuable goods and services, such as forage for cattle in a pasture sown with *C. ciliaris*, and the cost of restoring this pasture is high. Another straightforward-certain example is where restoration to a natural ecosystem is attempted because the value of a novel system is low and the cost of its control is also low (Fig. 6b, cell 3), such as a small *Opuntia* invasion that can be biologically controlled.

However, “retain novel system” and “attempt return to natural system” decisions become complex and uncertain for stakeholders in cases where small areas of novel ecosystems (e.g., *Eucalyptus* invasion along streams) have relatively low costs of restoration and a high value for some parties (Fig. 6b, cell 1). In this case, some stakeholder groups (e.g., timber interests, beekeepers) may argue for keeping the novel system but other groups (e.g., conservationists) desire an attempt to return to the

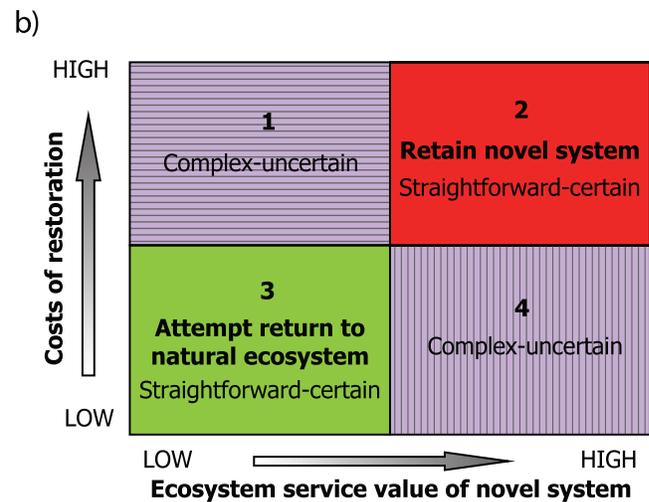
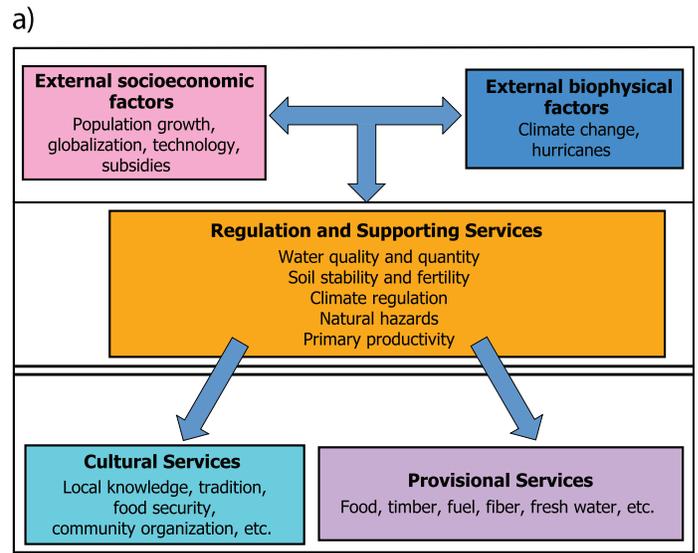


Figure 6. a, External drivers, both socioeconomic and biophysical, influence regulating and supporting ecosystem services, which in turn affect cultural and provisional services. b, A framework to aid stakeholders in deciding management actions. Decisions on how to manage novel systems are based weighing the cost of restoring a novel ecosystem versus the value of its services (supporting, regulating, cultural, and provisional). When costs and benefits are conflicting (high cost-low value of novel system [cell 1] or low cost-high value of novel system [to at least some parties] [cell 4]), then land management decision making is complex and uncertain, and resolution of costs versus benefits by societal (stakeholder) groups becomes important. Novel ecosystems are retained when their value is high and the cost of restoring them is also high (cell 2) or restored to natural systems (cell 3) when the value and restoration costs of the novel system is low.

natural state, resulting in conflicts that would need to be resolved as part of the land management decision-making process. These decisions may be extremely difficult, especially when the value of the novel ecosystem is extremely high to some stakeholders but the exotic species involved is highly invasive.

Complex and uncertain decisions also apply when an unintentionally created novel ecosystem has low value of services and costs of restoration are very high (Fig. 6b, cell 1), such as controlling the infectious invader rinderpest. In this

case, the size of the infected area may influence managers to argue for a “do-nothing” or “live-with-it” decision. In the case of large infestations of *C. ciliaris*, living with it may still require managing novel fuels and fire risks within and adjacent to urban areas. In cases where the affected area is relatively small and the danger of large-scale invasion is high (e.g., pockets of *C. ciliaris* within a nature park), some managers may argue for control despite costs. Benefits and restoration costs are currently high for *C. ciliaris* pastures in Australia, Texas, and Sonora, although the cost of managing novel fire regimes and loss of native plants and wildlife could eventually exceed the benefits to livestock. In southern Arizona, United States, *C. ciliaris* is not actively planted or grazed by livestock, so any benefits to novel ecosystems are principally hypothetical (e.g., reduced soil erosion).

Another complex–uncertain example is the expansion of woody plants into rangelands. Once woody cover reaches a critical threshold, restoration to the former grassland community can be very difficult and expensive for large areas. Rather than attempt restoration, in many cases these new woodlands are now actively managed with the use of integrated shrub management approaches (e.g., thinning woody plants, planting understory species, etc.) to maximize multiple ecological benefits that include nitrogen fixation, shade for livestock, habitat for wildlife, and may also increase property values (Archer et al. 2011). In other cases, woody expansion may be in its early phases, such as in the tall grass prairie in the Great Plains of the United States, and restoration is achievable.

MANAGEMENT IMPLICATIONS

As we have documented in the case studies, introduced alien and expanding native species can play a vital and positive role or have severe negative consequences in rangelands worldwide. Whether intentional or not, the encroachment of certain species may increase in the future, especially as anthropogenic disturbances increase (Ewel et al. 1999), whereas many native species will decrease or go extinct. Given the uncertainty of future conditions, the lack of past analog communities or climates and the increased and wide variety of demands being placed on rangelands (Stafford Smith et al. 2009), management of these novel ecosystems will become ever more difficult (Seastedt et al. 2008). As a rule of thumb, we suggest that when the presence of a species threatens the regulating and supporting services of the ecosystem (Fig. 6a), the case for eradicating the species (if possible) or altering the mechanisms that enhance its success is strong (Seastedt et al. 2008). If it does not threaten the supporting and regulating services or only does so in localized areas, or if it threatens provisioning or cultural services, retention of the species can be a societal decision based on cost–benefit analyses and conflict–resolution processes (e.g., stakeholder workshops).

As future conditions may not allow a return to the past ecosystem or even the attainment of a desired future, a new focus on novel ecosystem processes, resilience, and adaptability with a diversity of approaches will be required (Holling 2001; Hobbs et al. 2010). Thus, most management actions can be viewed as experimental, calling for a strong alliance among policy makers, managers, scientists, and the public, so that

success of actions can be evaluated from multiple viewpoints (Seastedt et al. 2008; Sayre et al. 2012 [this issue]) and best meet the needs of all concerned parties.

ACKNOWLEDGMENTS

We thank Margaret Friedel for her input to the ecology and management of invasive weeds in Australia, Elisabeth Huber-Sannwald for providing Figure 6a, Jeff Martin for editorial assistance, and the helpful comments from two anonymous reviewers.

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