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Effects of Invasive Alien Plants on Fire Regimes

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Plant invasions are widely recognized as significant threats to biodiversity conservation worldwide. One way invasions can affect native ecosystems is by changing fuel properties, which can in turn affect fire behavior and, ultimately, alter fire regime characteristics such as frequency, intensity, extent, type, and seasonality of fire. If the regime changes subsequently promote the dominance of the invaders, then an invasive plant–fire regime cycle can be established. As more ecosystem components and interactions are altered, restoration of preinvasion conditions becomes more difficult. Restoration may require managing fuel conditions, fire regimes, native plant communities, and other ecosystem properties in addition to the invaders that caused the changes in the first place. We present a multiphase model describing the interrelationships between plant invaders and fire regimes, provide a system for evaluating the relative effects of invaders and prioritizing them for control, and recommend ways to restore preinvasion fire regime properties.

Keywords: disturbance, fire frequency, fire intensity, fuel, nonnative plants

Invasions by alien plants are a growing challenge worldwide to the management of native biodiversity and ecosystem functioning. Invasive alien plants can directly affect native plants by becoming either monopolizers or donors of limiting resources. They can also indirectly affect native plants and change ecosystems by altering soil stability; promoting erosion; colonizing open substrates; affecting the accumulation of litter, salt, or other soil resources; and promoting or suppressing fire (Vitousek 1990, Richardson et al. 2000). The effects of invaders are particularly dramatic when they alter disturbance regimes beyond the range of variation to which native species are adapted (e.g., D'Antonio et al. 1999), resulting in community changes and ecosystem-level transformations (Mack and D'Antonio 1998).

Invaders that alter fire regimes are widely recognized as some of the most important system-altering species on the planet (Vitousek 1990, D'Antonio and Vitousek 1992, D'Antonio 2000). An example of a widespread invader that

has caused tremendous changes in fire regimes and other ecosystem properties is the alien annual grass *Bromus tectorum* in western North America. Its invasion across this vast landscape has increased fire frequency to the point that native shrub–steppe species cannot recover (Whisenant 1990). This, in turn, negatively affects animals that require this habitat type for forage and cover. These include the sage grouse (*Centrocercus urophasianus*) and species such as the black-tailed jackrabbit (*Lepus californicus*) and Paiute ground squirrel (*Spermophilus mollis*), which are major prey items for golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) (Knick et al. 2003). Efforts to restore native plant communities and preinvasion conditions in this shrub–steppe system may be hampered by changes in the spatial and temporal distributions of soil nutrients as well as the high density of the invader's seed bank. The invasion of *Bromus rubens*, another nonnative grass, into the Mojave Desert of western North America poses similar threats to fire regimes,

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native plants, and the federally threatened desert tortoise (*Gopherus agassizii*) (Brooks and Esque 2002). Thus, plant invasions that alter fire regimes can have repercussions that ripple throughout ecosystems, and these multiple effects may complicate the task of restoring ecosystems to preinvasion conditions.

Some of the effects of plant invasions on fire regimes have been previously described (e.g., D'Antonio and Vitousek 1992, Mack and D'Antonio 1998, D'Antonio 2000), but these examples largely focus on one well-known type of change, namely, grass invasions that increase fuel-bed flammability, and on the positive feedback cycle that can develop between invasive grasses and the frequency, size, spatial pattern, and, in some cases, intensity of fires. There are other important ways in which plant invaders can affect fuels and fire regimes, but these have not been documented as thoroughly, either because they have not yet been studied or because they are less common.

In this article, we describe the full range of pathways through which plant invaders can change fuel properties and, in doing so, alter fire regimes. It is not our purpose to conduct a thorough review of this topic. Rather, we present a general conceptual model of the invasive plant–fire regime cycle that summarizes the various possible interrelationships between invasive plants, fuels, and fire regimes, including indirect links through native plants and other ecosystem properties. We also present a system designed to help managers determine what can be done at various phases of the invasive plant–fire regime cycle to prevent further changes and reverse the changes that have already occurred.

What is a fire regime, and why is it important?

Fire is a type of disturbance (*sensu* Sousa 1984), and ecosystems are partly defined on the basis of disturbance regimes of specific frequency, intensity, extent, type, and seasonality (*sensu* Pickett and White 1985) (figure 1). Fire frequency

may be defined as a measure of the fire cycle (average time for fire to burn an area equal in size to the given area of interest) or of the fire return interval (average time before fire re-burns a given area, also called the fire recurrence interval). We use the latter definition in this article. Fire intensity, the amount of heat released per unit of time, is related to fire severity, which is the effect of this heat release on biotic and abiotic ecosystem properties. Fire extent includes both the size and the spatial homogeneity of burning. Fires have traditionally been classified according to fire type, which includes the categories of ground fire (e.g., peat-bog fires), surface fire (e.g., grass fires), and crown fire (e.g., forest-canopy fires). Seasonality refers to the annual window of fire activity and is largely determined by the ability of fuels to ignite and carry fire.

Disturbance regimes affect ecosystem properties such as the rates of soil erosion or formation and the pathways and temporal patterns of nutrient cycling and energy flow. Disturbance regimes can also act as a selective force affecting the life-history traits of individual species and the composition, structure, and emergent properties of entire groups of organisms. Over evolutionary time, fire regimes can promote coexistence of plant species, with different life forms dominating at different stages of postfire succession (Cowling 1987).

Fire regimes are affected by spatial and temporal variations in topography, climate, and fuel (figure 1). Although topography changes over geologic time, regional climate can potentially shift within the scale of centuries to decades, and fuel conditions can change within a day following a major disturbance. Rapid fuel changes can also rapidly change microclimates within vegetation stands. Fuels are the one ecosystem component that is inextricably linked with fire regime by feedback loops through other ecosystem properties and plants (figure 1). Shifts outside the natural range of fuel conditions can result in directional shifts in fire behavior and fire regime

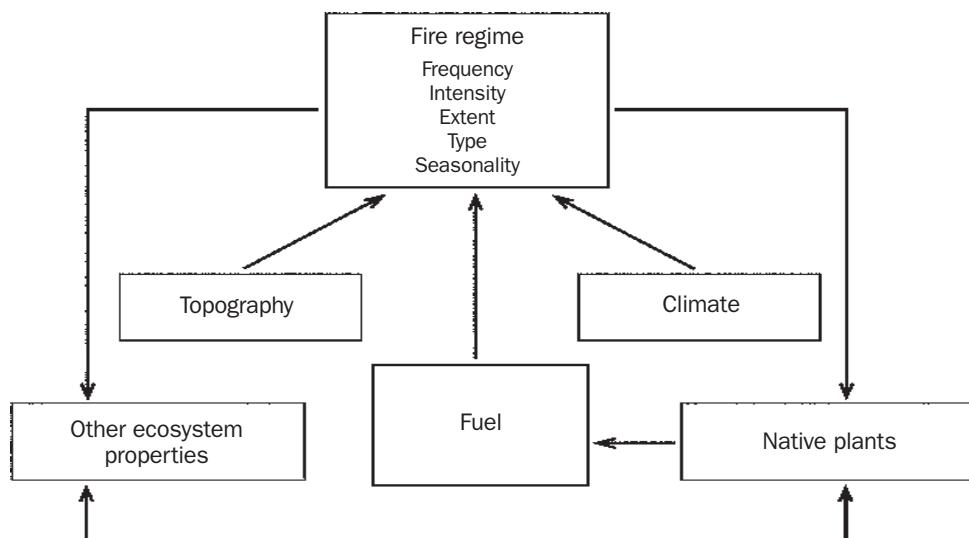


Figure 1. The fire regime cycle before plant invasion.

properties, which may result in localized extirpation of species that cannot persist under the new regime. The new fire regime, coupled with the localized loss of native plant species, creates opportunities for other species to colonize or expand their cover in sites they could not previously dominate. Many invasive alien species are well suited for rapid dispersal into altered landscapes and persistence under altered disturbance regimes (D'Antonio et al. 1999). In fact, invasive plants can first cause altered fire regimes by changing fuel conditions and then flourish under the new conditions they create.

Fuel properties and their effects on fire regimes

Fuels are generally categorized into types based on the predominant physiognomic structure of the vegetation (e.g., grassland, shrubland, or forest fuels). These types are further defined by various combinations of fuel "layers," based on their vertical arrangement on the landscape (e.g., ground, surface, or crown fuels). Fuel types and fuel layers directly influence the types of fire that can occur. For example, crown fires cannot occur without crown fuels. In addition, crown fuels must either be continuous enough to carry fire on their own (e.g., an active crown fire) or be supplemented by surface and ladder fuels (flammable material extending between surface and crown fuels) that carry fire along the surface between crown gaps and then from the surface back into the crown (e.g., a passive crown fire). This example does not begin to consider the various other fuel properties that can affect fire behavior and ultimately fire regimes. To accurately evaluate the effects of fuels on fire regimes, one must consider more detailed intrinsic and extrinsic properties of fuels.

Intrinsic fuel properties are those that are characteristic of the plants themselves. These properties primarily affect fire frequency, intensity, and seasonality (table 1). One such property is fuel moisture content (DeBano et al. 1998). Physiological condition and phenological stage of development affect the moisture content of live plant tissue. In contrast, the moisture content of dead tissue is affected by the ratio between the surface area of a fuel particle and the volume of that particle, which is often classified into various stem-diameter size classes (e.g., time lag moisture classes; DeBano et al. 1998). The more fuel volume is exposed to the external environment, the more rapidly the fuel's moisture content increases or decreases in response to changes in environmental moisture levels (e.g., relative humidity). As fuel moisture declines, so too does the amount of heat required from an ignition source to ignite the fuel. Two other intrinsic fuel properties are the chemical volatility and heat content of plant tissue (DeBano et al. 1998). These relate to the ignitability of fuel and the amount of heat produced when it burns.

Extrinsic fuel properties are those that relate to the way plants are arranged on the landscape. These properties can affect all aspects of the fire regime (table 1). They include the amount of fuel per unit area, the small-scale packing ratio of fuel, and the fuel continuity within a site and across the landscape (DeBano et al. 1998). The amount of fuel, typically referred to as the fuel load, is one of the primary determinants

of fire intensity. The packing ratio is the amount of fuel per unit volume of space, which affects the rate of fuel combustion. For a given fuel type, combustion is maximized at a particular ratio of fuel to oxygen. Departures above or below this ratio reduce the combustion rate and thus the ignitability and flammability of fuels, affecting fire frequency, intensity, and seasonality. Horizontal fuel continuity affects the frequency of fire and its extent as it spreads across the landscape. Vertical fuel continuity affects fire type (e.g., surface fire versus crown fire) as the fire spreads vertically from ground fuels, through ladder fuels, and up into the canopy.

Plant invasions have the potential to cause rapid directional changes in all of the above fuel properties, and thus to alter fire regimes, especially when multiple invaders act synergistically to accelerate change. In perhaps most cases, plant invasions that change fire regimes do so by altering more than one fuel and fire regime property. For example, grass invasions of shrublands, such as the *B. tectorum* invasion described earlier, increase fire frequency by increasing the fuel surface-to-volume ratio, increasing horizontal fuel continuity, and creating a fuel packing ratio that facilitates ignition. At the same time, these invasions generally decrease, and change the spatial pattern of, fire intensity and soil heating as discontinuous, woody shrubland fuels are replaced by more continuous, herbaceous grassland fuels. In the following sections, we describe in more detail the various ways plant invasions can change intrinsic and extrinsic fuel properties and thus alter fire regimes.

Effects of plant invasions on intrinsic fuel properties and fire regimes

Plant invasions often involve the establishment of new life forms which may have intrinsic fuel properties that differ from those of native species. However, relatively few such cases of altered intrinsic fuel properties have been reported in the literature.

Moisture content of plant tissue. Invasion of stem-succulent plants into shrublands increases the moisture content of live fuels, potentially making it more difficult for fire to ignite and spread. In California, the South African succulent *Carpobrotus edulis* invades postfire chaparral in maritime regions (Zedler and Scheid 1988). This species, in turn, negatively affects the recruitment and growth of native shrub species (e.g., D'Antonio and Mahall 1991), eventually leading to a conversion of maritime chaparral to a mix of succulent- and shrub-dominated vegetation. Although fuel characteristics of these vegetation types have not been explicitly compared, this community change should lead to increased live fuel moisture levels and reduce fuel combustion rates, fire spread rates, and fire intensity. Similar changes may occur as species of the stem succulent *Opuntia* invade Mediterranean shrublands in Europe and elsewhere.

Invasion of the nitrogen-fixing tree *Myrica faya* into grass-dominated sites in Hawaii is likely to decrease the rate of fire spread, because *Myrica* typically maintains higher fuel mois-

Table 1. Methods by which plant invasions can change fuel and fire regime properties.

| Fuel property changed | Fire regime properties changed | Examples |
|-------------------------------------|--|--|
| Intrinsic fuel properties | | |
| Increased plant tissue flammability | Increased fire frequency and intensity, and increased annual window of fire activity | Trees: <i>Eucalyptus</i> spp. in North America (possible, but not documented) |
| Decreased plant tissue flammability | Decreased fire frequency and intensity, and decreased annual window of fire activity | Succulents: <i>Opuntia</i> spp. in Europe (possible, but not documented) Herbs: <i>Centaurea maculosa</i> in North America (Xanthopoulos 1988) Shrubs/trees: <i>Acacia saligna</i> in Africa (van Wilgen and Richardson 1985); <i>Myrica faya</i> in the South Pacific (Tim Tunison, Hawaii Volcanoes National Park, Honolulu, Hawaii, personal communication, 14 October 2003) |
| Extrinsic fuel properties | | |
| Increased fuel load | Increased fire intensity | Perennial grasses: <i>Andropogon gayanus</i> in Australia (Rossiter et al. 2003); <i>Andropogon virginicus</i> , <i>Schizachyrium condensatum</i> , <i>Melinis minutiflora</i> , and <i>Hyparrhenia rufa</i> in the South Pacific (Smith and Tunison 1992) Trees: <i>Melaleuca quinquenervia</i> in North America (Gordon 1998) |
| Decreased fuel load | Decreased fire intensity | Annual grasses: <i>Bromus</i> spp. and <i>Avena</i> spp. in North America (Keeley 2001) |
| Increased horizontal continuity | Increased fire frequency and extent | Annual grasses: <i>Bromus tectorum</i> (Whisenant 1990), <i>Bromus rubens</i> , <i>Schismus</i> spp. (Brooks 1999), and <i>Taeniatherum caput-medusae</i> (Young 1992) in North America Perennial grasses: <i>Andropogon gayanus</i> (Rossiter et al. 2003), <i>Pennisetum polystachyum</i> (Gill et al. 1990), and <i>Cenchrus ciliaris</i> (Latz 1991) in Australia; <i>Hyparrhenia rufa</i> in Central America (Bilbao 1995); <i>Lolium perenne</i> (Zedler 1983) in North America; <i>Hyparrhenia rufa</i> , <i>Melinis minutiflora</i> , <i>Panicum Maximum</i> , and <i>Brachiaria</i> spp. in South America (Blydenstein 1967); <i>Andropogon virginicus</i> , <i>Schizachyrium condensatum</i> , <i>Melinis minutiflora</i> , and <i>Hyparrhenia rufa</i> in the South Pacific (Smith and Tunison 1992) |
| Decreased horizontal continuity | Decreased fire frequency and extent | Shrubs: <i>Mimosa pigra</i> in Australia (Braithwaite et al. 1989) Trees: <i>Schinus terebinthifolius</i> (Doren and Whiteaker 1990) and <i>Sapium sebiferum</i> (Grace 1998) in North America |
| Increased vertical continuity | Surface fire to crown fires | Vines: <i>Cryptostegia grandiflora</i> in Australia (Grice and Brown 1996) Herbs: <i>Chromolaena odorata</i> in Africa (Richardson et al. 1997) Perennial grasses: <i>Andropogon gayanus</i> (Rossiter et al. 2003) in Australia; <i>Imperata cylindrica</i> (Lippincott 2000) and <i>Arundo donax</i> (Bell 1997) in North America |
| Decreased vertical continuity | Crown fire to surface fires | Annual grasses: <i>Bromus</i> spp. and <i>Avena</i> spp. in North America (Keeley 2001) |
| Change in packing ratio | Change in fire frequency, intensity, and annual window of fire activity | Shrubs: <i>Acacia saligna</i> and <i>Hakea sericea</i> in Africa (van Wilgen and Richardson 1985) Trees: <i>Sapium sebiferum</i> (Grace 1998) in North America |

ture than the dominant native grasses. Furthermore, in closed stands, the moisture content of *Myrica* leaf litter can be very high because of the high relative humidity in the subcanopy, which reaches 50% to 60% (Tim Tunison, Hawaii Volcanoes National Park, Honolulu, personal communication, 14 October 2003). However, extreme drought conditions could change these relationships.

Invasions by finely textured plants such as grasses typically produce standing dead fuels that dry rapidly in response to low soil moisture and atmospheric humidity, promoting fire ignitions earlier in the spring and later in the fall. Thus, these invasions increase the length of the fire season and may also increase the probability of ignition during the heart of the fire season. Even within postfire chaparral environments, alien grasses have a very different phenology than the native herba-

ceous flora. Alien grasses germinate in the fall and dry by early spring, in contrast to the native flora, which germinates in the winter and remains green much longer. Thus, alien grasses extend the fire season earlier into the spring months in chaparral (Keeley 2000). Invasions of coarsely textured woody species into grasslands may have the opposite effect (e.g., Drewa et al. 2001).

Chemical composition of plant tissue. Fuel chemistry may be important in promoting fire spread, if it results in slower or more rapid decomposition rates of plant tissue and therefore in higher or lower levels of dead fuel biomass during the fire season. In addition, chemical compounds in plants may either increase plant flammability (e.g., volatiles) or decrease it (e.g., minerals), all other fuel characteristics being equal.

However, some investigators have determined that differences in fuel chemistry between invaders and natives are typically small and may have little to do with observed variation in fire intensity (van Wilgen et al. 1990, Lippincott 2000). Essentially, these researchers suggest that other fuel properties have more influence on fire regimes.

Effects of plant invasions on extrinsic fuel properties and fire regimes

New plant life forms introduced through invasions can change extrinsic fuel properties of vegetation stands. These types of changes have been more extensively documented than changes in intrinsic fuel properties caused by invasions.

Fuel loads. Increased fuel loads can increase fire intensity. Bilbao (1995) reports that African grass invaders can increase grass biomass by 50% in grass-dominated Venezuelan savannas, and that this results in hotter fires in these already fire-prone ecosystems. Likewise, invasion by the large African bunchgrass *Andropogon guyanus* into otherwise shorter-statured Australian savannas causes enormous increases in fuel loads, resulting in much hotter fires (Rossiter et al. 2003). Invasions of Hawaiian ecosystems by perennial alien grasses increase the load of fine fuels (e.g., litter, grass) and the fire intensity, eliminating fire-sensitive native species (Smith and Tunison 1992, D'Antonio et al. 2000). Although increased fuel loads generally lead to increased fire intensity, the ultimate effects also depend on the cumulative effects of other fuel properties such as the size class of the fuel, its packing ratio, and its moisture content.

Plant invasions can also decrease fire intensity when they lead to vegetation type conversions that result in plant assemblages with lower fuel loads or less flammable fuels. For example, annual grass invasions into the chaparral and coastal sage scrub of western North America have led to fuel type conversions that changed crown fire regimes, which spread entirely through shrub canopies, to mixed regimes of surface and crown fires (Keeley 2001). Fire frequency has also increased, which helps maintain the lowered fuel loads, both by preventing the accumulation of fuels over time and by promoting the persistence of early-successional herbaceous species. Invaders can also decrease the biomass of surface fuels by shading out the understory, and therefore decrease fire intensity and the probability of fire spread, particularly if their own leaves and twigs have higher fuel moisture than the native fuels (e.g., Doren and Whiteaker 1990, Lonsdale and Miller 1993).

Fuel continuity. Increased horizontal fuel continuity can increase the frequency and extent of fire. For example, the annual grass *B. tectorum* has increased fuel continuity in sagebrush shrublands of western North America, because it can germinate and grow under harsh conditions typical of the interspaces between shrubs. This has been associated with increased occurrence of wildfire and decreased occurrence of native species (Whisenant 1990, Brooks and Pyke 2001). In

contrast, woody shrub invasions into grasslands can reduce the horizontal continuity of fuels, reducing fire frequency and extent (Drewa et al. 2001). The invasive tree *Sapium sebiferum* can overtop and suppress the growth of understory coastal prairie species in North America, reducing the continuity of highly flammable surface fuels and thus the frequency of fire (Grace 1998).

Horizontal fuel continuity can affect how wind moves across the vegetation canopy, which in turn can influence the rate of fire spread. In Hawaiian seasonally dry forests, for example, sites dominated by exotic grasses, where the native over-story has been lost, have greater wind speeds compared with nearby sites where native woody species are still abundant (Freifelder et al. 1998). This can lead to increased rates of fire spread, making containment of fire more difficult and ultimately increasing the frequency and extent of fire.

The addition of ladder fuels increases vertical fuel continuity, allowing fires to travel from the surface into the crowns of shrubs and trees. This may not affect the frequency of fires, but it can affect their intensity and perhaps their spatial extent. Increased vertical fuel continuity has resulted from the invasions of the vine *Chromolaena odorata* in South African savannas (Richardson et al. 1997), the herbaceous shrub *Cryptostegia grandiflora* in Australia (Grice and Brown 1996), the tallgrass *Arundo donax* in Californian riparian habitats (Bell 1997), and the large bunchgrass *Imperata cylindrica* in pine savannas of the southeastern United States (Lippincott 2000). These invasions have shifted the surface fire regime to a crown fire regime.

Shifts from surface to crown fire regimes may also occur when an invader changes the predominant fuel type from surface to crown fuels, reducing the frequency of surface fires and allowing crown fires to occur only during extreme fire weather and fuel conditions. Examples include the invasion of grasslands by the trees *Schinus terebinthifolius* and *S. sebiferum* in North America (Doren and Whiteaker 1990, Grace 1998), and the shrub *Mimosa pigra* in Australia (Lonsdale and Miller 1993). In contrast, shifts from crown to surface fires can occur when the predominant fuel type changes from crown fuels to surface fuels. One example is the shift from the continuous crown fuels and discontinuous surface fuels in North American chaparral to the discontinuous crown fuels and continuous surface fuels created by invasive annual grasses (Keeley 2001).

Fuel packing ratio. Changes in fuel packing ratios can either increase or decrease fuel flammability, depending on the optimal ratio for combustion of a given fuel type. For example, grass invasions into shrublands, or shrub invasions into grasslands, can change the fuel packing ratio, respectively increasing and decreasing the chance of fire. In a simulation of fire spread in South African fynbos, van Wilgen and Richardson (1985) found that invasion by the shrub *Hakea sericea* resulted in reduced rates of fire spread rates because the fuel bed was so densely packed that combustion was inhibited, even though the invasion increased fuel loads by 60%. Nonethe-

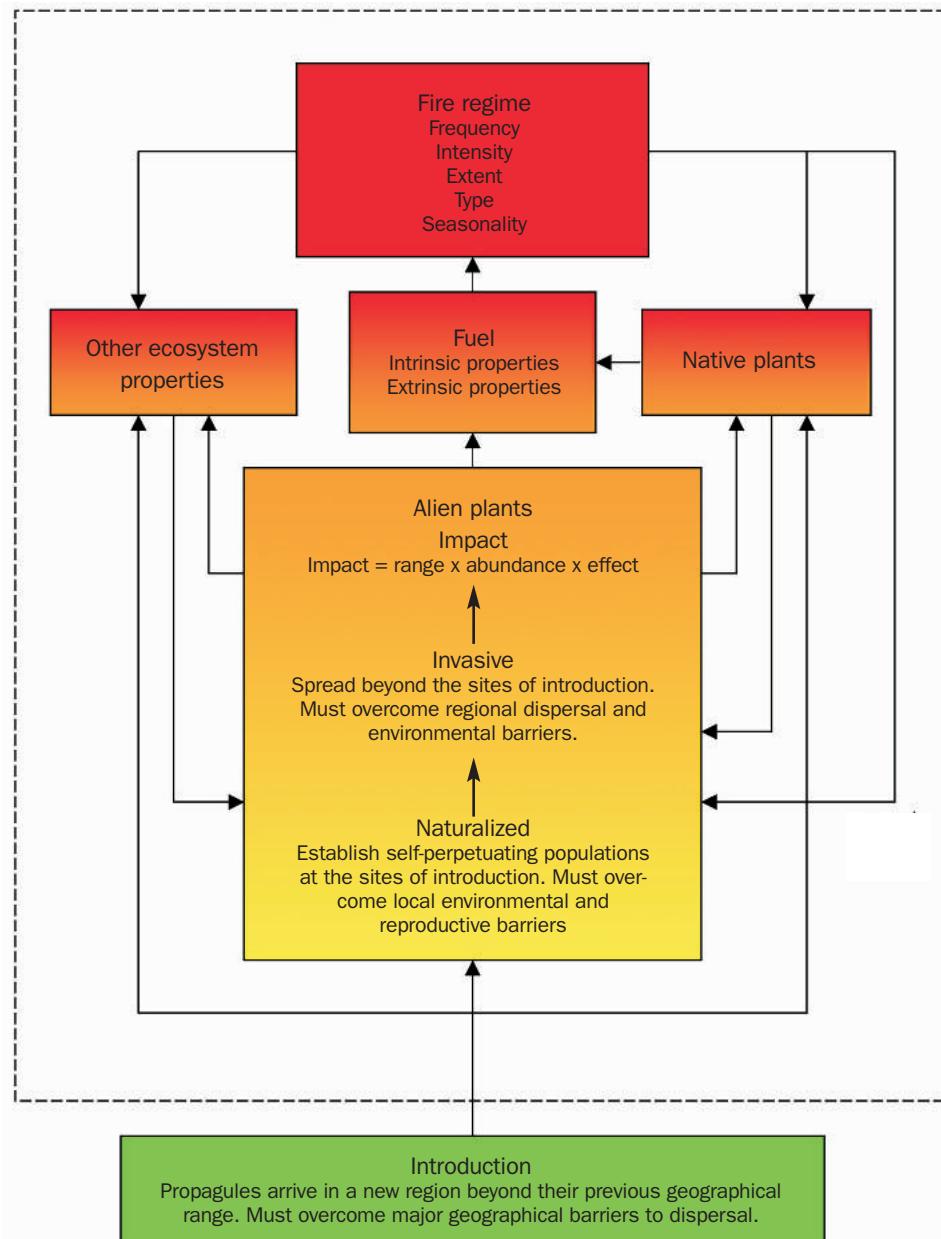


Figure 2. The invasive plant–fire regime cycle. Green, phase 1; yellow, phase 2; orange, phase 3; red, phase 4.

less, using the same simulation models, these authors concluded that fires can spread during extreme weather conditions, and the increased fuel load can result in fires that are much more intense than in uninvaded sites.

The invasive plant–fire regime cycle

Fuel properties can be directly changed by the addition of invasive plants (e.g., Whisenant 1990) or indirectly changed by alteration in the amount and species composition of native plants, caused by the competitive effects of the invaders (D'Antonio et al. 1998). Fuels are also affected by alterations to ecosystem properties (e.g., nitrogen cycling, soil organic matter) that feed back to affect vegetation, and especially by

the dominance of the invasive plant species. Whatever the mechanisms, the effects of invaders will be transient unless the invader can persist and thrive under the new conditions its presence has helped create. Invaders can shift fire regimes into self-perpetuating, alternative stable states (*sensu* Westoby et al. 1989) only when there is a net positive feedback between the regime characteristics and the invading species.

We present a multiphase conceptual model describing these dynamics, which we call the invasive plant–fire regime cycle (figure 2). This is an expansion of the grass–fire cycle of D'Antonio and Vitousek (1992) and takes into account the wide range of possible interrelationships between invasive plants, fuels, and fire regimes.

Phase 1. To fully understand the invasive plant–fire regime cycle, one must first consider the evolutionary history of potential invaders and the habitats they may invade, in addition to their fuel characteristics. Species' adaptations to specific fire regimes within their native range may shed light on their ability to persist under similar fire regimes elsewhere. For example, an annual species that evolved with frequent fire may be adapted to establish and reproduce rapidly after fire and may include a self-burial mechanism for its seeds to protect them from mortality during subsequent fires. This type of species would be preadapted for similar frequent, low-intensity fire regimes elsewhere, whether these regimes were naturally created by native fuels or altered as a result of changes in fuel structure caused by plant invasions. The ability of an invader to eventually create a self-sustaining invasive plant–fire regime cycle depends on its ability to persist under the new regime it creates. These and other considerations are critical in prescreening species for possible exclusion from management regions, as we discuss in more detail later in this article.

Phase 2. The second phase of the cycle is the introduction of propagules into a new region, which requires the invader species to overcome significant geographical barriers to dispersal (Richardson et al. 2000). If additional barriers to survival and reproduction can be overcome, then the species can naturalize, establishing self-perpetuating populations. Many populations of alien species do not spread away from localized habitats such as roadsides, urbanized or agricultural areas, and the margins of ecological regions with harsh environmental conditions (e.g., deserts). Species that can overcome these dispersal and environmental barriers become invasive (*sensu* Richardson et al. 2000). Fire or other disturbances that can reduce the vigor of resident plants and their ability to resist invasion, or alter environmental conditions to favor invaders, may shorten the phase between establishment and spread (e.g., King and Grace 2000).

Landscape patterns can greatly affect the invasion process. For example, the mosaic patchwork of oak savanna and chaparral in the foothills of the Sierra Nevada in North America places alien-dominated savannas in close proximity to largely uninvaded chaparral. Following fire, the extent of alien invasion into chaparral is largely a race between aliens reaching the site and shrublands returning to their former closed-canopy condition (Keeley et al. 2003). Fire extent can affect this process, because the large perimeter-to-area ratio of small burns can make areas more vulnerable to invasion than larger fires (Turner et al. 1997).

Phase 3. The third phase of the cycle occurs when invasive plant species reach sufficient abundance across a large portion of an ecosystem to change native population, community, or ecosystem properties. Parker and colleagues (1999) suggest an integrated measure that is helpful in summarizing the primary factors associated with an invader's total

ecological impact in phase 3 of our model. They propose the equation

$$I = R \times A \times E,$$

where I is invader impact, R is geographical range (e.g., square kilometers), A is abundance (in numbers, biomass, etc.), and E is per capita effect. Thus, within a geographical location, the abundance needed to cause significant ecological impact is a function of the per capita effect, which refers to the specific effect of the invader within the context of the invaded ecosystem. Changes brought about by plant invasions may affect native plant and ecosystem properties, and create new fuel conditions that can alter fire behavior, but the fire regime is not altered until changes in fuel and fire behavior persist over subsequent fires in phase 4 of our model.

Phase 4. The final phase in this model, which completes the invasive plant–fire regime cycle, involves the perpetuation of altered fuel conditions and fire behavior characteristics over subsequent fire return intervals. At this point, the fire regime is said to be changed. The new regime persists as long as it positively reinforces the range, abundance, or effect of the invading species. This positive feedback may involve the elimination of the resident plants. For example, if the native plants recover from fire more slowly than the invaders, or if reduced fire frequency allows the invaders to overtop natives and drive them out, the invaders benefit from a less competitive environment under the altered fire regime. This feedback may also be enhanced if fire increases soil nutrient availability, promoting the growth and reproduction of invasive plants. Fire regimes can also benefit invading species directly. For example, decreased fire frequency and intensity may benefit invading species that are poorly adapted to frequent fire (e.g., *S. sebiferum*; Grace 1998), or increased fire frequency and intensity may benefit invaders that are fire resistant. In summary, if invaders alter a fire regime, and if the net effects of the altered regime on the invaders are positive, then an invasive plant–fire regime cycle is created.

Preventing or mitigating the invasive plant–fire regime cycle

Management of invasive plants can occur at any spatial scale, from an entire continent to a small plot of land. Most commonly, these species are managed at the scales of individual nations, states or territories, counties or townships, and parks or reserves. Systems designed to evaluate the effects of plant invasions and prioritize them for control should ideally be independent of spatial scale or, at least, be directly applicable to the various spatial units at which invasive plants are commonly managed. We present such a system for evaluating and prioritizing invasive plants at each of the four phases leading to the establishment of an invasive plant–fire regime cycle (figure 3).

Species that are not yet introduced. The most effective way to prevent invasive plants from altering fire regimes is by preventing their initial introduction. This requires pre-

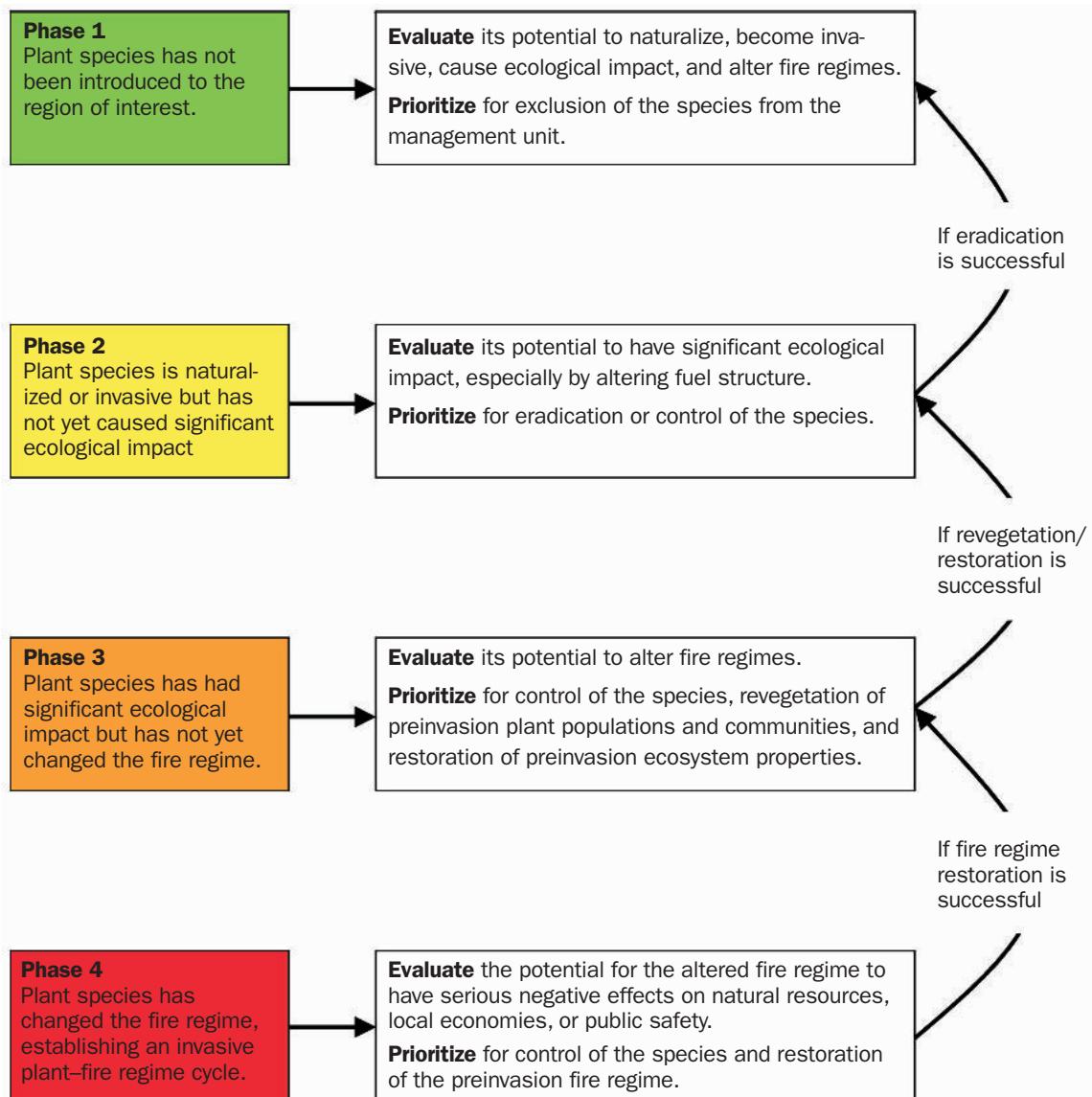


Figure 3. A system to evaluate the effects of invasive species and prioritize them for control and restoration of preinvasion conditions at various stages of the invasive plant–fire regime cycle.

screening criteria that include the potential for species to alter fuel and fire regime characteristics in the management region of interest. Plant species that have not yet invaded a region need to be evaluated for their potential to naturalize, become invasive, cause ecological impact, and eventually alter fire regimes (figure 3). Species with a high potential to alter fire regimes should be prioritized for exclusion from the region. Prescreening species to determine whether their introduction should be prevented is typically done at the national level. In the United States, preventing the introduction of potentially fire regime–altering plants does not effectively occur, because the interdiction at points of entry focuses on species legislated as federal noxious weeds (see www.aphis.usda.gov/ppq/weeds/noxiousweedlist.pdf), and this list does not generally include fire-altering species. The same can be said for the exclusion of these species from most

states, because interdiction at that scale focuses on state-listed noxious weeds. Noxious weeds are typically listed because of their threats to agriculture, aquatic systems, and other economic sectors, and not because of their threat to ecosystem properties such as fire regimes. Two plant-screening systems proposed for Australia (Virtue et al. 2001) and for the South African fynbos (Tucker and Richardson 1995) include potential effects of fire regimes; however, these systems have not yet been implemented at national scales.

Naturalized or invasive species. Species that have naturalized or become invasive need to be evaluated for their potential to cause significant ecological impact (figure 3). Species with a high potential to cause a negative impact need to be prioritized for control. These species often qualitatively change ecosystem properties. For example, a nitrogen-fixing shrub

Box 1. Management options for breaking the invasive plant–fire regimes cycle and restoring the pre-invasion fire regime.

If invaders promote any aspect of fire regime, then consider:

Managing fuels

- Eradicating or reducing the dominance of the invaders that alter fuel structure.
- Vegetating with fire-resistant plants that can compete with invaders and reduce their effects on the fuelbed.
- Creating firebreaks by green-stripping or mechanical methods to protect native landscapes from recurrent fire.
- Manipulating other ecosystem properties/processes necessary to restore preinvasion vegetation and fire regime characteristics.
- Limiting land-use activities that increase the dominance of invaders and their effects on fuelbeds and fire regimes, while promoting those that reduce invader effects.

Managing ignition sources

- Adopting local ordinances to reduce the frequency of ignitions by humans.

If invaders suppress any aspect of fire regime, then consider:

Managing fuels

- Eradicating or reducing the dominance of the invaders that alter fuel structure.
- Vegetating with plants that restore preinvasion fuel structure, or otherwise increase its flammability.
- Using mechanical or chemical treatments to increase fuel flammability.
- Manipulating other ecosystem properties/processes necessary to restore preinvasion vegetation and fire regime conditions.
- Limiting land-use activities that increase the dominance of invaders and their effects on the fuelbed and fire regime, while promoting those that reduce invader effects.

Managing ignition sources

- Using prescribed fire after the fuelbed has been altered to increase its flammability.
- Using prescribed fire when weather conditions permit burning (e.g., high winds, high temperature, low humidity).

that invades a grassland with no native nitrogen fixers could qualitatively change both fuel-bed structure and soil nutrient cycling, which in turn may negatively affect native plant species and confound revegetation efforts. Alternatively, species that only cause quantitative ecosystem changes may be less likely to cause significant ecosystem impact. For example, alien annual grasses invading native annual grasslands may not dramatically affect fuel beds or other ecosystem properties, although relatively large quantitative changes can have significant negative ecosystem effects (e.g., Mack et al. 2001).

Species with significant ecological impact. Species that have already caused significant ecological impact, but have not changed the fire regime, need to be evaluated for their potential to alter fuels and fire regimes under any of the environmental conditions that occur in the region (figure 3). Species with a high potential to alter fire regimes should be prioritized for control. In addition, restoration of preinvasion plant community and ecosystem properties may be necessary. In general, species that introduce qualitatively novel fuel characteristics should be considered greater threats than those that may only quantitatively change fuel conditions. An invasion that introduces a novel fuel type could be a tree or shrub in-

vading a grassland, whereas an invasion that only quantitatively changes an existing fuel type could be an annual grass invading a grassland. If the invader has also significantly altered native plant populations or communities, or changed ecosystem properties other than fire regimes, then additional effort may be required to restore native species and preinvasion native fuel conditions.

Species that have changed the fire regime. When a species has already changed one or more characteristics of the fire regime, the altered regime needs to be evaluated for its potential to have negative effects on natural resources, local economies, and public safety (figure 3). Such effects on the landscape may include loss of wildlife habitat, promotion of subsequent invasions by other alien species, altered watershed functioning, loss of tourist appeal, and increased fire-associated hazards. Species with a high potential to cause negative effects through altered fire regimes need to be prioritized for control, and the preinvasion plant community, fuel, fire regime, and other ecosystem properties need to be restored.

A range of management options are available that may mitigate the negative effects of altered fire regimes and restore plant communities to preinvasion conditions (box 1). The options used depend on whether the invader is a fire promoter

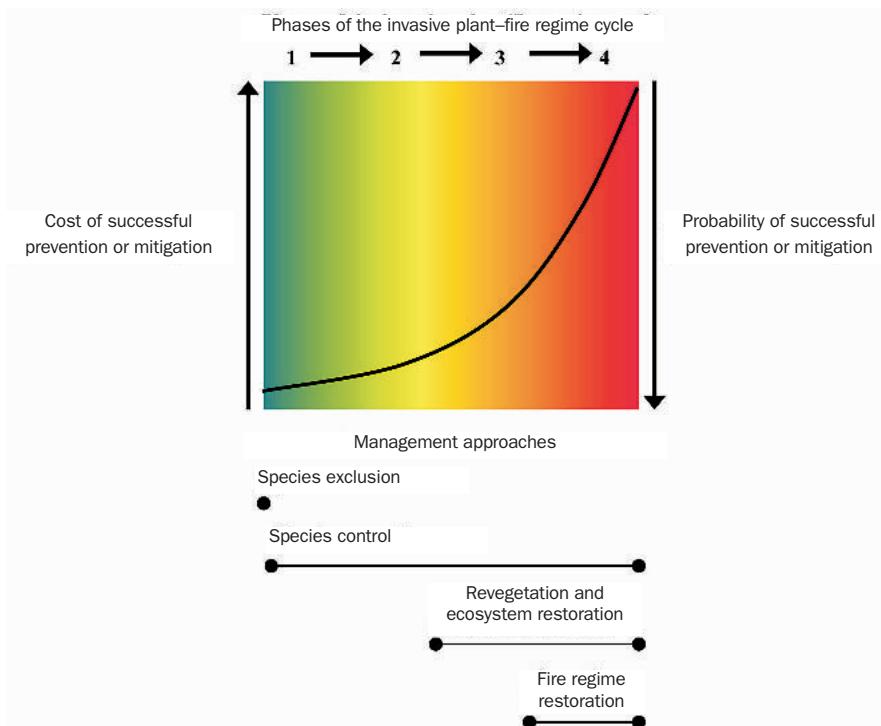


Figure 4. Relative cost and probability of success for management actions designed to prevent or mitigate the invasive plant–fire regime cycle.

or fire suppressor, whether there is remaining native habitat that can be protected, and to what extent a native species pool exists that can be used for restoration or revegetation.

Restoration of preinvasion conditions can often require managing both fuels and ignition sources (box 1). For example, mature stands of *Sa. sebiferum* that invade prairie ecosystems suppress fire by shading out understory surface fuels (Grace 1998). When these stands are removed using mechanical or chemical treatments, native surface fuels often recover on their own to the point where fire can be reintroduced. Periodic burning at preinvasion return intervals can then be used to benefit native prairie species and kill small size classes of encroaching *Sa. sebiferum* trees (Grace 1998).

In other cases, it may not be possible to restore communities to their preinvasion state. For example, fire-enhancing tropical grasses from Central America and Africa have invaded seasonally dry habitats in the Hawaiian Islands. The increased occurrence of fire has resulted in the complete loss of native forest in some regions, but not in others, because of differences in the native species pool (D'Antonio et al. 2000). In seasonally dry habitats where the native forest has disappeared with increased fire frequency, Tunison and colleagues (2001) found that it was not possible to restore the original native species, and instead created new assemblages of native species that are fire tolerant and can coexist with the native grasses. In other circumstances, alien species may be used in postfire revegetation to compete with invaders and re-create preinvasion fuel characteristics that help restore altered fire regimes. For example, alien species such as the bunchgrass *Agropyron deser-*

torum have been seeded into postfire landscapes in the Great Basin desert of North America to suppress growth of the alien annual grass *B. tectorum* and thereby reduce fuel continuity and flammability (Hull and Stewart 1948). The use of one alien species to reduce the negative ecological effects of another is often controversial, and at the very least, the long-term effects of such practices should be carefully considered beforehand.

The costs and probabilities of successful prevention or mitigation efforts

One of the few certainties of invasive plant management is that exclusion of potentially threatening species before they invade, or at least early detection and rapid response at the very early stages of invasion, is the most cost-effective and successful way to prevent their negative ecological and economic impacts (Naylor 2000, Rejmánek and Pitcairn 2002). This is especially true in the prevention and mitigation of the invasive plant–fire regime cycle (figure 4). During phase 1, management approaches can completely focus on exclusion of the invasive species. There may be economic costs associated with exclusion (e.g., for ornamental horticulture or livestock forage plants), but these costs are often dwarfed by the potential long-term costs of inaction. In addition, the cost of control is lowest, and the probability of successful management is highest, during this initial phase. When a species is introduced and becomes invasive during phase 2, management costs begin to rise and the probability of successful prevention or mitigation of negative effects begins to decline, but

management can still focus entirely on the invasive species. In contrast, once phase 3 begins, management must focus not only on the invader but also on revegetating altered plant communities and restoring altered ecosystem processes. Phase 4 adds the task of restoring preinvasion fire regimes. Thus, at each subsequent phase of the invasive plant–fire regime cycle, additional management considerations are added, costs increase, and the probability of successful management decreases (figure 4). At the latter stages of this cycle, it will do little good to focus only on controlling the invader if the native fire regime, other ecosystem properties, and native plant communities need to be restored as well.

Summary

Plant invasions can affect native ecosystems in many different ways, and effective management is greatly facilitated when the mechanisms that promote invasion and lead to subsequent ecological impacts are understood. We have presented a general conceptual model describing interrelationships between plant invasions and fire regimes. Many of these relationships are not widely recognized, such as the potential ways that plant invasions can suppress fire. One of the purposes of this article was to highlight all the possible interrelationships between plant invasions and fire regimes, so that land managers and others will take them into consideration when they design systems for screening potential new invaders before introduction and for setting priorities to manage invasions that have already occurred.

To take our predictive power to the next level, it would be particularly useful if we could compare the relative threats posed by different types of changes in fuel structure brought about by plant invasions. For example, under what conditions is fuel continuity rather than fuel load more important in altering fire regimes, and when do changes result in significant ecological or economic impacts? Clearly there is much that we still do not know about the effects of plant invasions on fire regimes and about managing both the invading species and the altered fire regime. We hope the information presented in this article will help to spark new research evaluating the ways that invading plants affect fuel properties and fire regimes. Research should focus both on the mechanisms by which invasive plant–fire regime cycles become established and on the management tools that can be used to reverse these changes or otherwise mitigate their negative effects.

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