

# Impacts of biological invasions on disturbance regimes

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Recent research shows that the disproportionate effects of a single plant functional group may best predict the effects of biodiversity on ecosystem function<sup>1,2</sup>. Ecosystem-level fluxes of energy and matter can be altered by organismal traits such as plant litter quality (review in Ref. 3), resource acquisition by plants or animals (e.g. Refs 4–6), or microclimatic factors that modulate rates of ecosystem processes<sup>7</sup>. Some species interact strongly with the disturbance regime of an ecosystem. Because disturbance represents a primary control over the variance of ecosystem processes in time, these species can also have strong effects on ecosystem processes<sup>8</sup>. Growing evidence suggests that the removal or addition of species that interact strongly with disturbance regimes often results in discrete state changes in ecosystem structure and function. Biological invasions represent the addition of a new species identity into an ecosystem; thus, they offer model systems for understanding the mechanisms by which species or functional groups alter disturbance regimes.

New evidence suggests that invaders alter disturbance regimes in both disrupted and intact systems, and that in many cases these alterations result in profound changes, including direct species replacements and changes in ecosystem processes that ultimately control plant and animal activity. Invasion can result in a positive feedback between disturbance and the abundance of non-native species, such as the positive feedback observed between some introduced grasses and fire<sup>5</sup>. Alternatively, invasion may result in feedbacks that lead to depression or removal of the invader from the system<sup>9</sup>.

It is well known that invasions can be promoted by disturbance<sup>10,11</sup>, but it is less generally recognized that invaders can alter disturbance regimes (but see Refs 5,7) because causality is often difficult to determine<sup>12</sup>. Invaders that are initially promoted by an outside disturbance can maintain the system in an altered state, or introduce a qualitatively new type of disturbance and further change the system. In cases where invaders establish without disturbance (or with a minimal level of disturbance) alterations to the disturbance regime also occur. Causality is much clearer in these cases.

Here we review new and accumulated evidence that individual species in terrestrial ecosystems can cause profound and often irreversible alterations to those systems. We uncovered 58 studies from throughout the world where invaders are associated with subsequent changes in disturbance

**Human management activities have altered the frequency and intensity of ecosystem disturbance often with enormous impacts on landscape structure and composition. One additional and under-appreciated way in which humans have altered disturbance regimes is through the introduction of invasive non-native species, themselves capable of modifying existing disturbance regimes or introducing entirely new disturbances. In many cases, modifications of disturbance regimes results in maintenance of ecosystems in a new or transitional state. There is now evidence that alteration of disturbance regime may be the most profound effect that a species or functional group can have on ecosystem structure and function.**

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regime<sup>12</sup>. These include examples where invaders changed physical or biological aspects of the disturbance, and/or changed the response of the biota to disturbance (Table 1). Invaders either introduce, enhance or suppress events such as fire and erosion, or are themselves agents of disturbance—disrupting the soil or sediment, or killing a significant fraction of the community in a relatively short period of time. They can also change the consequences of the disturbance force by changing the aggregate response or range of responses of the biotic community. Our review covers the most common mechanisms through which invaders alter disturbance regimes, emphasizing ways in which ecosystems are being changed in previously unrecognized ways. We use Sousa's<sup>13</sup> definition of disturbance as a punctuated event or series of events that kill or damage existing organisms, directly or indirectly increase resource availability and create an opportunity for new individuals to become established.

## Invaders that interact with physical forces of disturbance

### Fire enhancement

Recently, D'Antonio and Vitousek<sup>7</sup> suggested that grass invasions create feedbacks that cause potentially irreversible alterations in the fire regime in many invaded ecosystems. We identified 14 regionally or taxonomically distinct cases in which grass invasions increased the frequency and/or intensity of fire. In at least two cases (Refs 14,15), initial disturbance was not required to set the cycle in motion.

**Table 1. How invaders alter disturbance regimes**

Alteration	Example	Refs
Fire enhancement	Grasses increase rates of fire frequency, spread, and/or areal extent	14,15
Fire suppression	Trees decrease fine fuel load and fire spread in grassland or open woodland	20–22
Increased erosion	Trees increase stream bank collapse in riparian zones	24
Decreased erosion	Plants stabilize mobile substrates	9,26,27
Increased biotic disturbance	Pigs increase soil disturbance	6,29,30,33,37
Increased biotic disturbance	Pests or pathogens cause stand-level or population-level dieback	43,44
Change in consequences of disturbance	Invader changes susceptibility of community to physical forces of disturbance	47–49

The high surface area:volume ratio of grass leaves and typical accumulation of dead biomass increase the probability of fire particularly in ecosystems that previously lacked a large grass component. Grass and/or fire feedbacks have been documented in many parts of the world. We now recognize that in western USA they are responsible for large-scale conversion of mixed shrub-steppe vegetation to stands of introduced annual grasses in the Great Basin<sup>14</sup>. In Hawaii Volcanoes National Park, both fire frequency and extent have increased since grass invasion<sup>15</sup>; and in seasonal submontane woodlands, fires clearly promote the spread and thickening of introduced grasses<sup>16</sup>. These grasses create a homogeneous canopy compared to native forest, promoting higher wind speeds and greater rates of fire spread<sup>17</sup>.

Promotion of fire by invaders has also been suspected in some ecosystems where woody invaders occur. For example, in South African fynbos, the Australian shrub *Hakea sericea* increases fuel loads and decreases average live fuel moisture content, yet simulated fire spread rates under moderate weather were lower than in uninvaded shrubland due to differences in fuel-packing density<sup>18</sup>. Sites invaded by the shrub *Acacia saligna* also had higher fuel loads than uninvaded sites, but fuel moisture was greater. Hence, model predictions under moderate weather were again similar for invaded and uninvaded sites. Under extreme weather conditions, however, fire intensity was higher in invaded versus pristine fynbos<sup>18</sup>, and intense fires have occurred in invaded sites. They are thought to stimulate germination and possibly facilitate the establishment of new stands of invaders<sup>19</sup>.

#### Fire suppression

Few published studies correlate presence of plant invaders with suppression of existing fire regimes (Refs 20–23). Those available involve invasion by woody species into mesic or flooded grassland sites where invaders then suppress understory fuel development<sup>20–23</sup>. In Australian flood plains invaded by the shrub *Mimosa pigra*, fires have been observed to go out as they enter *M. pigra* thickets<sup>21</sup>, where understory biomass is lower than beneath native shrubs<sup>22</sup>. The invasion of *M. pigra* leads to a decreased frequency and intensity of early dry season fires – when these woodlands have historically burned<sup>22</sup>. The pepper tree, *Schinus terebinthifolius*, invades fire-maintained prairies and abandoned farmland in Florida. Mature stands can have densities up to 11 355 stems ha<sup>-1</sup>, with almost complete suppression of understory grasses<sup>20</sup>. Doren and Whiteaker<sup>20</sup> found that the reduction in fine fuels beneath *S. terebinthifolius* canopies depressed fire intensity and spread. These effects could benefit recruitment and survival of *S. terebinthifolius* because young seedlings are fire sensitive and adults are killed by crown fires<sup>20</sup>.

#### Increased geomorphological disturbance

Introduced species may affect geomorphology of the invaded site by altering substrate stability directly or by influencing the composition of the understory or litter layer, in turn affecting erosional processes. *Acacia mearnsii*, an Australian invader of South African ecosystems, increases stream bank erosion due to relatively easy uprooting during high flow periods<sup>24</sup>. Macdonald and Cooper<sup>25</sup> attribute this to its lower root investment and more shallow root system compared to dominant native species. Post-flood river banks are rapidly colonized by exotic species<sup>25</sup>.

#### Decreased geomorphological disturbance

There are many examples of plants that bind and stabilize disturbed substrates, thus reducing the frequency

or intensity of natural disturbances and potentially leading to accelerated succession. Grasses with extensive root systems are used to stabilize landslides and eroded hillslopes, mining and construction scars, other human-disturbed sites and sand dunes. Clonally-growing species that ramify via stolons or rhizomes are particularly successful at stabilizing disturbed and mobile substrates. Some species introduced for substrate stabilization have become invaders of natural ecosystems. For example, European beach grass, *Ammophila arenaria*, alters dune formation patterns where it has invaded in North America<sup>26</sup>, New Zealand and Australia<sup>27</sup>. In southern Australia, *A. arenaria* is more efficient at trapping sand than native beach grasses, and results in new foredune formation and larger dune size than dunes formed by native grasses<sup>27</sup>. The consequences of these changes for native species are largely unknown.

The impacts of introduced species on substrate stability may extend across ecosystems. For example, the invasion of South African fynbos by a suite of woody invaders has resulted in a 3- to 10-fold increase in above-ground biomass<sup>18</sup>. Increased transpiration of intercepted rainfall has led to a 50% decrease in flow levels of some stream catchments, which would reduce sedimentation, erosion and in-stream disturbances.

Substrate stabilization by invaders can lead to accelerated rates of succession. Bermuda grass (*Cynodon dactylon*) invades stream courses in Arizona and influences community development by increasing substrate stability<sup>9</sup>. Sites dominated by *C. dactylon* retained more substrate during floods, including basal fragments of native aquatic macrophytes. Post-flood development of the aquatic macrophyte community proceeded more quickly in these sites than in those lacking *C. dactylon*. Overgrazed and eroded hillslopes in Tunisian woodlands are invaded by *Pinus halepensis*, which stabilizes soil and enhances establishment of native shrubs and trees<sup>33</sup>.

#### Invaders that are biotic disturbance agents

##### Pigs

The European pig (*Sus scrofa*) is currently found on all continents except Antarctica, and on many oceanic islands, and is the most obvious example of how an invading animal that is not reliant upon disturbance to invade a system can directly alter a disturbance regime. By grubbing for roots, underground stems, and macroinvertebrates, pigs can till large areas of soil resulting in plant death<sup>29</sup>, root death<sup>6</sup>, mixing of soil horizons<sup>6,29,30</sup>, increased rates of nutrient mineralization<sup>5,6</sup>, and decreased rates of nitrogen retention<sup>6</sup>. In Californian coastal prairies, pigs disturb 7.4% of the surface area each year, while native soil disturbers (e.g. gophers) turn over <1% of meadow areas<sup>29</sup>. Pig-grubbing is associated with a depression of soil micro- and macroarthropod numbers<sup>6,30</sup>, but may also be associated with increased macroinvertebrate numbers<sup>31</sup>.

Pig invasion into forested communities often results in the removal or replacement of the herbaceous understory<sup>32,33</sup>. Removal of the understory may alter ecosystem nutrient retention<sup>6,32</sup>, and lead to more rapid decomposition of soil organic matter<sup>6</sup>. Singer *et al.*<sup>6</sup> compared soil characteristics before pig invasion and 10 years later in a Tennessee forest and found a 65% decrease in soil organic matter and significant leaching of base cations and nitrogen from the soil profile. They also found elevated nitrogen in groundwater from watersheds where pigs had rooted. In contrast, pig impacts on grasslands do not appear to be large<sup>34</sup>.

### Other large feral animals

Feral goats and sheep have severely altered island ecosystems<sup>35,36</sup> where they are suspected of contributing to soil disturbance and loss. However, most studies of these animals have focused on their impacts on endangered native island species and not on their role in altering disturbance cycles or promoting further invasions. Spatz and Mueller-Dombois<sup>37</sup> found that the removal of feral goats led to a decline in introduced annual grasses and an increase in native woody perennials and introduced fire-promoting perennial grasses<sup>15</sup>. Thus, although the initial impact of goats is often difficult to assess, elimination of goats may lead to increases in fire frequency and further invasion by introduced grasses.

There is also evidence that feral ungulates can cause a decline in above-ground biomass production, thus causing a change in disturbance regimes in fire-prone ecosystems. The introduction of livestock grazing into the western United States corresponds to a decrease in fire frequency in western coniferous forests due to decreases in understory fuel<sup>38</sup>.

Feral Eurasian water buffalo (*Bubalus bubalis*) have been found to increase invasion by annual plants in Northern Territory, Australia because of their soil-disturbing activities<sup>39</sup>. Russell-Smith and Bowman<sup>33</sup> reported that soil damage caused by water buffalo was present in all but one of 16 different vegetation types in this area and 20% of over 1000 sites they surveyed were impacted by water buffalo. However, the long-term ecosystem consequences of water buffalo disturbance and the plant species they appear to promote are unknown.

### Small herbivores and detritivores

Small herbivores and detritivores have been implicated in changed disturbance regimes, including altered substrate mixing<sup>40,41</sup>, large-scale seed depredation<sup>42</sup>, and stand-level dieback<sup>25,43,44</sup>. In New Zealand pastures, European earthworms (Lumbricidae) significantly increased decomposition and plant production through their effects on soil mixing<sup>40</sup>. In contrast, European earthworms in the North American tallgrass prairie reduced soil turnover and nutrient mineralization compared to the native earthworm species (Megascolecidae) they are replacing<sup>41</sup>. In many systems, exotic herbivorous insects can initiate a boom-and-bust cycle of stand-level dieback. North American bark beetles (*Ips* spp) have caused increased tree death following fires in tropical pine forests<sup>43</sup>. Dieback of many North American hardwoods has been associated with outbreaks of the European Gypsy moth (*Lymantria dispar*)<sup>44</sup>. In both of these examples, stand regeneration occurs following collapse of pest populations. *Leucaena leucocephala*, an invasive shrub on many oceanic islands, underwent severe dieback when the psyllid bug *Heteropsylla cubana* was introduced from Middle America<sup>25</sup>. Ten years after introduction of the psyllid in Hawaii, however, some stands have increased dramatically to cover greater area than before dieback<sup>45</sup>.

### Invaders that affect the consequences of disturbance

Some invaders introduce a qualitatively new response to a disturbance, often concurrent with the introduction of a new disturbance regime. This appears to be particularly true where introduced grasses have created a grass/fire cycle<sup>7</sup>. For example, *Schizachyrium condensatum*, a Central American grass that has invaded Hawaiian woodlands, not only increases the frequency and size of fires, but regenerates rapidly from basal meristems following intense fire. Few of the dominant native species are able to do so, and introduced grasses increase their dominance after fire<sup>7</sup>.

Introduced plant species in grazing land ecosystems often introduce a qualitatively different suite of traits that interact with the biological disturbance of grazing. There are many examples where invaders with thorns, prickles, or chemical defenses have reduced the impact of grazers on a system and led to the abandonment of pastures<sup>46</sup>.

Invaders that differ subtly from natives can change community response to disturbance as well, although these responses in terms of community structure are also likely to be subtle. Caldwell *et al.*<sup>47</sup> compared the response to grazing of a native grass and its exotic congener and found that the canopy of the exotic recovered more quickly from grazing and had a higher photosynthetic capacity in new tissue than did the native species. With heavy livestock grazing, this and other native grasses are being replaced over much of their range by the exotic species<sup>47</sup>. In South African fynbos, Australian *Banksia* spp and exotic *Pinus* spp respond to fire by seeding more prolifically than native species, leading to their replacement<sup>43</sup>. Macdonald *et al.*<sup>49</sup> surveyed Reunion island after a cyclone and found that many of the exotic species were more damaged than native species. The only native trees to show heavy damage were either in thickets of the exotic shrub *Lantana camara*, or had the exotic canes of *Rubus alceifolius* intertwined in their canopies. By being more sensitive to damage and making natives more susceptible, in this case, invaders may change the outcome of disturbance.

### Invasion and disturbance: understanding the effects of changing species composition on ecosystem function

Disturbance is widely assumed to promote biological invasions<sup>12</sup>. In turn, invaders can cause changes in disturbance regimes that profoundly alter the composition and successional trajectory of a community, and development of the ecosystem. Disturbance regimes are a primary control over the variances of ecosystem processes in time. Hence, invasion-driven alterations of disturbance dynamics are examples of important single-species impacts on ecosystem processes<sup>8</sup>. As humans continue to move species around the globe and increase direct disturbances to ecosystems, the two-way link between disturbance and invasion will become even stronger. Introduced species now make up a substantial portion of the flora and fauna in many regions of the world<sup>50</sup> yet their impacts have rarely been systematically studied. In many of the studies reviewed here, positive relationships exist between the altered disturbance regime, the success of the invader, and the demise of some portion of the native assemblage. Most of these studies, however, only identify initial effects of alteration, cover a relatively short period, and do not explicitly identify effects on other ecosystem processes or changes in ecosystem structure and function. We require further research that builds on our current mechanistic understanding of disturbance alteration by following subsequent community and ecosystem changes over the time-scale of succession and ecosystem development.

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### References

- 1 Tilman, D. *et al.* (1997) **The influence of functional diversity and composition on ecosystem processes**, *Science* 277, 1300–1302
- 2 Hooper, D.U. and Vitousek, P.M. (1997) **The effects of plant composition and diversity on ecosystem processes**, *Science* 277, 1302–1305

- 3 Hobbie, S.E. (1992) **Effects of plant species on nutrient cycling**, *Trends Ecol. Evol.* 7, 336–339
- 4 Vitousek, P.M. *et al.* (1987) **Biological invasion by *Myrica faya* alters ecosystem development in Hawaii**, *Science* 238, 802–804
- 5 Vitousek, P.M. (1986) **Biological invasions and ecosystem properties: can species make a difference?** in *Ecology of Biological Invasions of North America* (Mooney, H.A. and Drake, J.A., eds), pp. 163–178, Springer-Verlag
- 6 Singer, F.J., Swank, W.T. and Clebsch, E.C. (1984) **Effects of wild pig rooting in a deciduous forest**, *J. Wildlife Manage.* 48, 464–473
- 7 D'Antonio, C.M. and Vitousek, P.M. (1992) **Biological invasions by exotic grasses, the grass/fire cycle, and global change**, *Annu. Rev. Ecol. Syst.* 23, 63–87
- 8 Vitousek, P.M. (1990) **Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies**, *Oikos* 57, 7–13
- 9 Dudley, T.L. and Grimm, N.B. (1994) **Modification of macrophyte resistance to disturbance by an exotic grass, and implications for desert stream succession**, *Proc. Inter. Asso. Theor. Appl. Limnol.* 25, 1456–1460
- 10 Hobbs, R.J. and Huenneke, L.F. (1992) **Disturbance, diversity, and invasion: implications for conservation**, *Conserv. Biol.* 6, 324–337
- 11 D'Antonio, C.M. and Dudley, T.L. (1995) **Biological invasions as agents of change on islands versus mainlands**, in *Islands: Biological Diversity and Ecosystem Function (Ecological Studies Vol. 115)* (Vitousek, P.M. *et al.*, eds), pp. 103–121, Springer-Verlag
- 12 D'Antonio, C.M., Dudley, T.L. and Mack, M.C. **Disturbance and biological invasions: direct effects and feedbacks**, in *Ecosystems of Disturbed Ground* (Walker, L., ed.), Elsevier (in press)
- 13 Sousa, W.P. (1984) **The role of disturbance in natural communities**, *Annu. Rev. Ecol. Syst.* 15, 353–391
- 14 Whisenant, S.G. (1990) **Changing fire frequencies on Idaho's Snake River Plain: ecological and management implications**, U.S.D.A., Forest Service, Intermountain Research Station
- 15 Smith, C.W. and Tunison, T. (1992) **Fire and alien plants in Hawai'i: research and management implications for native ecosystems**, in *Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research* (Stone, C.P. *et al.*, eds), pp. 394–408, University of Hawaii Press
- 16 Hughes, F., Vitousek, P.M. and Tunison, T. (1991) **Alien grass invasion and fire in the seasonal submontane zone of Hawaii**, *Ecology* 72, 743–746
- 17 Freifelder, R., Vitousek, P.M. and D'Antonio, C.M. **Microclimate effects of fire-induced forest/grassland conversion in seasonally dry Hawaiian woodlands**, *Biotropica* (in press)
- 18 Van Wilgen, B.W. and Richardson, D.M. (1985) **The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study**, *J. Appl. Ecol.* 22, 955–966
- 19 Holmes, P.M., Macdonald, I.A.W. and Juritz, J. (1987) **Effects of clearing treatment on seed banks of the alien invasive shrubs *Acacia saligna* and *Acacia cyclops* in the southern and south-western Cape, South Africa**, *J. Appl. Ecol.* 24, 1024–1051
- 20 Doren, R.F. and Whiteaker, L.D. (1990) **Effects of fire on different size individuals of *Schinus terebinthifolius***, *Nat. Areas J.* 10, 107–113
- 21 Lonsdale, W.M. and Miller, I.L. (1993) **Fire as a management tool for a tropical woody weed: *Mimosa pigra* in north Australia**, *J. Environ. Manage.* 33, 77–87
- 22 Braithwaite, R.W., Lonsdale, W.M. and Estbergs, J.A. (1989) **Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra***, *Biol. Conserv.* 48, 189–210
- 23 Darrow, W.K. and Zanoni, T. (1990) **Hispaniolan pine (*Pinus occidentalis* Swartz). A little known subtropical pine of economic importance**, *Commonw. For. Rev.* 69, 133–146
- 24 Macdonald, I.A.W. and Richardson, D.M. (1986) **Alien species in terrestrial ecosystems of the fynbos biome**, in *The Ecology and Management of Biological Invasions in Southern Africa* (Macdonald, I.A.W. *et al.*, eds), pp. 77–91, Oxford University Press
- 25 Macdonald, I.A.W. and Cooper, J. (1995) **Insular lessons for global biodiversity conservation with particular reference to alien invasions**, in *Islands: Biological Diversity and Ecosystem Function (Ecological Studies Vol. 115)* (Vitousek, P.M. *et al.*, eds), pp. 189–203, Springer-Verlag
- 26 Wiedemann, A.M. and Pickart, A. (1996) **The *Ammophila* problem on the northwest coast of America**, *Landscape Urb. Plan.* 34, 287–299
- 27 Heyligers, P.C. (1985) **The impact of introduced plants on foredune formation in south-eastern Australia**, *Proc. Ecol. Soc. Austr.* 14, 23–41
- 28 Wojterski, T.W. (1990) **Degradation stages of the oak forests in the area of Algiers**, *Vegetatio* 87, 135–143
- 29 Kotanen, P.M. (1995) **Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie**, *Ecography* 18, 190–199
- 30 Vtorov, I.P. (1993) **Feral pig removal: effects on soil microarthropods in a Hawaiian rain forest**, *J. Wildl. Manage.* 57, 875–880
- 31 Anderson-Wong, P. (1994) *A relationship between earthworms and feral pig activity in a Hawaiian rain forest*, Hawaii Conservation Conference, Honolulu, Hawaii
- 32 Aplet, G.H., Anderson, S.J. and Stone, C.P. (1991) **Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park**, *Vegetatio* 95, 55–62
- 33 Russell-Smith, J. and Bowman, D.J.M.S. (1992) **Conservation of monsoon rainforest isolates in the Northern Territory, Australia**, *Biol. Conserv.* 59, 51–63
- 34 Baron, J. (1982) **Effects of feral hogs (*Sus scrofa*) on the vegetation of Horn Island, Mississippi**, *Am. Midl. Nat.* 107, 202–205
- 35 Coblenz, B.E. (1978) **The effects of feral goats (*Capra hircus*) on island ecosystems**, *Biol. Conserv.* 13, 279–286
- 36 Van Vuren, D. and Coblenz, B.E. (1987) **Some ecological effects of feral sheep on Santa Cruz Island, California, USA**, *Biol. Conserv.* 41, 1987
- 37 Spatz, G. and Mueller-Dombois, D. (1975) **Successional patterns after pig digging in grassland communities on Mauna Loa, Hawai'i**, *Phytocoenologia* 3, 346–373
- 38 Savage, M. and Swetnam, T.W. (1990) **Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest**, *Ecology* 71, 2374–2378
- 39 Cowie, I.D. and Werner, P.A. (1993) **Alien plant species invasive in Kakadu National Park, tropical Northern Australia**, *Biol. Conserv.* 63, 127–135
- 40 Syers, J.K., Sharpley, A.N. and Keeney, D.N. (1979) **Cycling of nitrogen by surface casting earthworms in a pasture ecosystem**, *Soil Biol. Biochem.* 11, 181–185
- 41 James, S.W. (1991) **Soil, nitrogen, phosphorus, and organic matter processing by earthworms in a tallgrass prairie**, *Ecology* 72, 2101–2109
- 42 Chown, S.L. and Smith, V.R. (1993) **Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward islands**, *Oecologia* 96, 508–516
- 43 Goldammer, J.G. and Penafiel, S.R. (1990) **Fire in the pine-grassland biomes of tropical and subtropical Asia**, in *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges (Vol. 84)* (Goldammer, J.C., ed.), pp. 45–62, Springer-Verlag
- 44 Houston, D.R. (1981) **Effects of defoliation on trees and stands**, in *The Gypsy Moth: Research Toward Integrated Pest Management* (Doane, C.C. and McManus, M.L., eds), pp. 217–218, United States Department of Agriculture
- 45 Medeiros, A. (1991) *Management Plan for Kanio Natural Area reserve*, Cooperative National Park Studies Unit
- 46 Jayanth, K.P. and Ganga Visalakshy, P.N. (1996) **Succession of vegetation after suppression of parthenium weed by *Zygodrumma bicolorata* in Bangalore, India**, *Biol. Agric. Horticult.* 12, 303–309
- 47 Caldwell, M.M. *et al.* (1981) **Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses**, *Oecologia* 50, 14–24
- 48 Richardson, D.M., Cowling, R.M. and Le Maitre, D.C. (1990) **Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos**, *J. Veg. Sci.* 1, 629–642
- 49 Macdonald, I.A.W. *et al.* (1991) **Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean)**, *Environ. Conserv.* 18, 51–61
- 50 Vitousek, P.M. *et al.* (1996) **Biological invasions as global change**, *Am. Sci.* 84, 468–478