

The ecology and management of mammal invasions in forests

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Abstract Populations of invasive wild mammals have contributed significantly to the total unwanted impacts of biological invasions. They are known to impact forest ecosystems globally, but reviews summarizing this information are currently lacking. Here we (1) review the ecological characteristics of mammal invasions in forests; (2) characterize the range of ecological impacts on forest communities and the economic consequences of those impacts; (3) review what is known about interactions between the impacts of invasive mammals and other drivers of global change; and (4) consider the complex ecological and socio-economic challenges of simultaneously managing multiple invasive mammals and native biota affected by them. The unwanted impacts of invasive herbivores and predators are intensifying in many parts of the world and the need to manage their impacts to prevent further loss of indigenous biodiversity and damage to productive assets is greater than ever. However, management needs to be conducted within appropriate social, cultural, ethical, and animal welfare

frameworks. Achieving effective management of populations of mammals invasive in forest ecosystems will require the filling of many knowledge gaps, including: better understanding their impacts; strategic options and tactical solutions for managing them; and achieving social licence to operate.

Keywords Global change · Herbivory · Impacts · Indigenous ecosystems · Introduced species · Predation

Introduction

Introduced wild mammals contribute significantly to the total unwanted impacts of biological invasions. In the United States, for example, the estimated annual cost associated with introduced invasive mammals in the early-2000s was c. US\$37 billion or about 31% of the total costs for all invasive taxa (Pimental et al. 2005). Similarly, introduced terrestrial vertebrates in Europe have disproportionately large ecological (30%) and economic (39%) impacts, despite being the smallest taxonomic group of nonindigenous species (Vilà et al. 2010). While the greater proportional effects of introduced terrestrial vertebrates may be partly attributable to a research bias towards this group, its importance is highlighted by, for example, the devastating effects that invasive mammal predators have had on native prey globally (Blackburn et al.

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2004; Sax et al. 2007; Hilton and Cuthbert 2010), and the significant costs attributable to food consumption and destruction by introduced rats and mice (Stenseth et al. 2003; Pimental et al. 2005).

Human-mediated movement of mammals is a prehistoric phenomenon (e.g., Wilmshurst et al. 2008; Giovas et al. 2012), but it increased substantially with human exploration until the early twentieth century, and was particularly prevalent following establishment of acclimatisation societies (Mack et al. 2000; Long 2003; Simberloff et al. 2013). The reasons for introducing mammals to new locations were varied, and included: for food, hunting and sport; pet-keeping; commercial interests such as domestic stock; biocontrol of (usually) other introduced species; accidental introductions and escapees; and aesthetics (Long 2003). Mammals have not been introduced in comparable numbers to all continents, nor have those introductions resulted in similar proportions of invasive populations (Vitousek et al. 1996; Long 2003). However, relatively high proportions of introductions and subsequent successful invaders are found among some mammalian orders (Artiodactyla, Carnivora, Lagomorpha, and Perissodactyla) as a result of intentional and accidental liberations by humans (Clout and Russell 2007). Although introductions are not synonymous with invasion or impacts, nonindigenous species have a greater propensity for causing adverse ecological impacts than indigenous species. Proposals to introduce a new species or the detection of a recent introduction should thus be cause for concern (Vilà et al. 2010; Simberloff et al. 2013).

Aims and definitions

Forests are impacted by mammalian invaders, but this information has not been summarized or synthesised for this ecosystem type. Integrating such information would help the development of comprehensive forest management policies. Here we provide a global review of mammal invasions in forests, with emphasis on less well-documented ecological and management themes. Specifically, we (1) review the ecological characteristics of mammal invasions in forests; (2) characterize the range of ecological impacts on forest communities and the economic consequences of those impacts; (3) review what is known about interactions between the impacts of invasive mammals and other

drivers of global change; and (4) consider the complex ecological and socio-economic challenges of simultaneously managing multiple invasive mammals and native biota affected by them.

We define an introduced mammal as a population of a nonindigenous mammalian species that by intentional or accidental human assistance occurs outside its native range (Lodge et al. 2006). It becomes an invasive population if it spreads and maintains itself without human assistance (Richardson 2011; Simberloff et al. 2013). Alternative definitions do not have human-assisted introductions as a prerequisite (Colautti and MacIsaac 2004), but rather accept that populations of some species native to a given region can become invasive. This distinction is important because populations of indigenous forest-dwelling mammals can have significant unwanted impacts in newly-invaded adjacent communities. For example, populations of white-tailed deer (*Odocoileus virginianus*) have extended their geographic ranges northward into boreal forest, an ecosystem from which they were historically absent, with subsequent unwanted impacts on some plants and animals (Côté et al. 2004; Latham et al. 2011). While such range shifts are ecologically important, they are not the primary focus of this paper. We define an invasive forest mammal as a population of an introduced mammal that lives at least partly in forests; acquires all or some of the resources on which it depends from forests; and has ecological impacts in forests or spill-over impacts on adjacent habitats. We similarly use a broad definition for forest ecosystems—they are lands dominated by woody vegetation (>2 m in height), from open woodland (10–40% canopy cover) to dense forest (>70% canopy cover), and include plantation and natural forests (e.g., Loveland et al. 2000; Achard et al. 2002).

Ecological characteristics of mammalian invasions of forests

Determinants of invasion success

To our knowledge, there are no forest-specific reviews documenting what proportion of introductions of wild mammals resulted in successful invasions. Of the small number (18) of wild mammal species that have successfully established at more than 30 locations around the world (Long 2003), >75% live, at least

partly, in forests or woodlands, e.g., red deer (*Cervus elaphus*), feral pigs (*Sus scrofa*), feral goats (*Capra hircus*), American mink (*Neovison vison*), and Javan mongoose (*Herpestes javanicus*; sometimes considered conspecific with the small Asian or Indian mongoose, *H. auro-punctatus*), and accidentally introduced commensals such as black rat (or ship rat; *Rattus rattus*), Norway (or brown rat; *R. norvegicus*), Polynesian rat (*R. exulans*), and house mouse (*Mus musculus*) (Clout and Russell 2007).

All introduced populations—whether to forested habitats or otherwise—must establish before they can become invasive. Relative to other taxa, vertebrates have a high probability (c. 0.5) of establishing and spreading (Jeschke and Strayer 2005) and mammals are significantly more likely to establish and become invasive than birds (Jeschke 2008). Successful establishment is often attributable to the number of individuals involved in the introduction or ‘propagule size’ (Lockwood et al. 2005; Simberloff 2009) and the environment to which they are introduced (Duncan et al. 2014). Propagule size is important because the likelihood of extinction from demographic and environmental stochasticity and random catastrophes is inversely proportional to population size (Lande 1993). Empirical evidence for the importance of propagule size is well-established. For example, Forsyth and Duncan (2001) assessed the outcomes of introductions of 14 nonindigenous ungulates, primarily in forest and scrub habitats, in New Zealand. They showed that the 11 successful species were introduced in greater numbers than unsuccessful ones and that successful establishment was likely if the introduction comprised c. six or more individuals. Propagule size, number of release events, and environmental suitability were also found to be important factors for the establishment and spread of 40 introduced species of mammals in Australia (Forsyth et al. 2004). However, some species, such as the North American muskrat (*Ondatra zibethicus*) introduced in Europe, have established and become invasive from very small propagules—three females and two males in the muskrat case (Long 2003).

Species traits may also play a role in invasion success (Duncan et al. 2001). Evidence for an association between life-history traits and the probability of establishment and spread of mammals in forests is difficult to ascertain because many traits commonly included in analyses have proven to be

significantly correlated with propagule size, irrespective of whether or not phylogeny is taken into account (Cassey et al. 2004). Of 40 mammal species introduced into Australia—most of which occur in scrub or forests—migration was the only life history trait of those assessed that was significantly associated with establishment outcomes when phylogenetic relatedness was controlled for (Forsyth et al. 2004). If species were non-migratory in their native range they were more likely to establish than migratory species, possibly because the latter range over larger distances than sedentary species decreasing the probability of finding a mate and increasing the risk of extinction via Allee effects (Forsyth et al. 2004). Further, life history traits, particularly those associated with higher intrinsic rates of increase, were important in explaining patterns of spread for those introduced populations that established.

Competitive advantages of invasive species over indigenous ones may also contribute to invasion success in some systems. Replacement of red squirrels (*Sciurus vulgaris*) by eastern grey squirrels (*S. carolinensis*) in Europe is often cited as an example of a nonindigenous species that has a competitive advantage over an indigenous one (Bertolino et al. 2014). The mechanisms behind the successful invasion by grey squirrels are thought to be their ability to exploit food resources and to cope with a *parapoxvirus* more efficiently than their European cousin (Genovesi and Bertolino 2001; Tompkins et al. 2003). Similarly, introduced fallow deer (*Dama dama*) may outcompete introduced red deer in some New Zealand forests where the two species occur sympatrically, possibly because they can adapt better to living in areas where grasses are scarce (Nugent and Asher 2005).

Facilitative interactions involving invasive mammals

Scientists have long been aware of synergisms and mutualisms among introduced populations of non-indigenous plants and animals (Simberloff and Von Holle 1999; Richardson et al. 2000). Simberloff (2006) outlines degrees of facilitative interactions, starting with one species aiding another. In this case, the helper is unaffected or insignificantly harmed, whereas the recipient receives sufficient help to result in a net effect of increased invasion. Mutual facilitation is species helping each other, with a net effect of

increased invasion. Finally, if the net effect of facilitation results in an increasing rate of establishment of introduced species and/or an increased impact, it is a community-level phenomenon, referred to as invasional meltdown (Simberloff and Von Holle 1999). There are ample examples of introduced species facilitating one another's establishment, spread, and impacts, and we briefly review some examples.

Eastern grey squirrels introduced into South Africa from North America disperse the seeds of introduced pine trees (*Pinus* spp.) in the South African mountain fynbos and have been critical to their successful establishment and spread, even though there is no known population benefit for the squirrel (Richardson et al. 2000). Pine invasion has also been facilitated by dispersal of ectomycorrhizal fungi spores by invasive red deer and brushtail possums (*Trichosurus vulpecula*) in New Zealand (Wood et al. 2015) and by feral pigs, red deer, and fallow deer in Argentina (Nuñez et al. 2013). Omnivorous feral pigs are often involved in complex relationships with plant communities. In Hawaii, for example, pig populations benefit from the large amount of fruit produced by invasive banana passionfruit (*Passiflora mollissima*) and strawberry guava (*Psidium cattleianum*) and these plants benefit from seed dispersal by pigs (Ramakrishnan and Vitousek 1989; Lowe et al. 2000). Moreover, pigs disturb the forest floor with their rooting as they search for plant roots and invertebrates. In the Hawaiian example, earthworms, which are introduced, are eaten by pigs. The earthworms contribute to increased burial rates of nitrogen-rich litter around the introduced nitrogen-fixing tree *Myrica faya*, which may lead to invasion by previously nitrogen-limited plants (Vitousek and Walker 1989; Aplet 1990). Increased rooting by pigs looking for earthworms similarly creates a disturbance favoured by some introduced plants (Aplet et al. 1991), and alters recruitment of native seedlings (Krull et al. 2013).

Crego et al. (2016) provide evidence for a possible invasional meltdown in southern Chile. North American beavers (*Castor canadensis*), introduced to southern South America c. 70 years ago, spread quickly to occupy all suitable habitat and modify it by felling trees for food and building lodges and dams. Another introduced species, the North American muskrat, selects habitat modified by beavers rather than naturally flowing streams and they represent

>50% of biomass of the diet of a third introduced mammal, American mink. Crego et al. (2016) argue that engineering by beavers has changed native habitat from forests into wetlands and thus facilitated an increase in introduced grasses and rushes and muskrats that depend upon this vegetation. In turn, muskrats are sustaining inland populations of mink which have major impacts on indigenous biota, particularly birds and small rodents. This appears to be a community-level phenomenon, with beavers increasing the rate of establishment of introduced species and accelerating the unwanted impacts of the invasive species.

Irruptive and chronic invasions

Introduced mammal species that become invasive may go through irruptive oscillations, though the timelines associated with oscillations for different taxa can vary by orders of magnitude. Following introduction, an invasive population may rapidly increase in numbers (irrupt) before showing a marked decline initiated by overshooting resource availability (Caughley 1970). Some invasive populations subsequently persist at a chronic density lower than the peak of the initial irruption. For K-selected species, for example, there is little population fluctuation between years but they can swing upwards into a second, usually less severe oscillation, if they are not managed (Caughley 1970). These types of animals are considered chronic invaders because their impacts are long-term and ongoing (Parkes and Murphy 2003), though not necessarily severe. Red deer populations in New Zealand display this pattern (Riney 1964), as do some populations of deer in their native ranges, e.g., white-tailed deer in some parts of the USA (Webster et al. 2005).

At the other end of the spectrum, populations of some invasive mammals can show short-term fluctuations that vary by orders of magnitude, usually in response to environmental change or resource availability. Introduced invasive and indigenous small mammals with high intrinsic rates of increase can respond rapidly to pulses of resources in forests. Classic examples are irruptions of rodents following mast flowering and seeding in ecosystems ranging from bamboo forests (e.g., outbreaks of black rats following masting by *Melocanna baccifera*; Belmain et al. 2010) to deciduous and coniferous forest in North America (e.g., Ostfeld et al. 1996; Wolff 1996;

McShea 2000; Clotfelter et al. 2007), and New Zealand (Ruscoe and Pech 2010). These irruptions can be localised but several mechanisms—dispersal, predation or environmental disturbance (the Moran effect; Moran 1953)—have potential to synchronize irruptions over very large areas. In New Zealand, where climatic cues have been linked to beech (*Fuscospora* spp. and *Lophozonia* sp.) masts (Kelly et al. 2013) and thus to rodent irruptions (Holland et al. 2015), simultaneous irruptions of invasive rodents in the North and South islands support the Moran effect as the primary cause of spatial synchrony. However, in New Zealand mixed-species forests, which have more consistent food availability, irruptions of invasive rodents can be more frequent and persist longer than in forest dominated by a single tree species (Glen et al. 2013). Although impacts of irruptive invaders are often brief they can be severe, and include economic damage (e.g., loss of crops in farms close to bamboo forest in Asia; Belmain et al. 2010) and environmental damage, especially in forest ecosystems where indigenous flora (e.g., Sweetapple 2003) and fauna (e.g., Elliott et al. 2010) did not co-evolve with introduced mammals.

Biotic resistance to mammal invasions

The biotic resistance model predicts that invasions by nonindigenous species are more likely to occur in species-poor communities than species-rich ones (the vacant niche hypothesis) and oceanic islands compared with mainland (island susceptibility hypothesis) (Elton 1958). It is believed that the greater diversity of indigenous species or resident nonindigenous species in species-rich communities will prevent establishment of new invaders by prior occupancy of most (or all) niches (Elton 1958; Levine and D'Antonio 1999). Demonstrating occupancy or availability of niches in invasion biology has proven difficult (e.g., Mack et al. 2000). We could find no published evidence for biotic resistance to invasive mammals in forests with vacant niches, but resistance to plant invasions has been documented (Wiser et al. 1998; Iannone III et al. 2016). Moreover, there has been considerable debate about the effect of non-indigenous species introductions on regional-scale species richness (Sax et al. 2002; Gonzalez et al. 2016; Vellend et al. 2016). Often

indigenous species that become extinct are extirpated by nonindigenous predators and pathogens, not nonindigenous competitors (Blackburn et al. 2004; Sax et al. 2007). Although competition-induced extinctions may occur over longer periods of time than those caused by predation and disease, evidence suggesting that many communities are not saturated (Sax et al. 2007) lends support to the vacant niche hypothesis. Support for the hypothesis that species-poor communities (like islands) are more susceptible to invasions by nonindigenous species than are species-rich ones (like mainland) is far from universal (Sol 2000; Jeschke 2008), and species richness often has no significant effect if propagule size is accounted for (Cassey et al. 2004; Simberloff 2009). Although there is support for biotic resistance, the evidence is equivocal (Levine and D'Antonio 1999; Jackson 2015), i.e., as discussed above there is also evidence for invasional meltdown and other facilitative interactions (Simberloff 2006).

In an experimental test of biotic resistance in rainforest in south eastern Australia, Stokes et al. (2009) showed that resident populations of indigenous bush rats (*Rattus fuscipes*) can block invasion by functionally equivalent, similar-sized invasive black rats. In the northern Philippines, an island ecosystem with a very high level of mammalian endemism, endemic small mammals were resistant to invasion by nonindigenous species, especially in areas least disturbed by humans (Rickart et al. 2011). A meta-analysis focused on invasive animals globally supported the biotic resistance model (Jackson 2015). Invasive animals generally had neutral or negative impacts on one another, and Jackson (2015) argued that the mean negative effect of invaders on one another supports the idea of serial replacement, i.e., new invaders come to dominate a community by outcompeting earlier invaders (Lohrer and Whitlatch 2002). Henriksson et al. (2016) predicted that if invasion success and defence capacity (i.e., contribution to resistance) are correlated, and successful invaders also cause most impact (through replacing native species with low defence capacity), then community resistance should increase as species accumulate. Using freshwater fish introductions in Swedish lakes as a model, they found that species' invasion success was positively correlated with their defence capacity and impact, suggesting that these

communities will develop stronger resistance over time.

Are some forests more likely to be invaded by mammals?

Forests and woodlands are highly diverse, ranging from tropical to temperate regions. Some are natural and relatively pristine, whereas some are regenerating following historic logging or natural disaster, or have a high human footprint as a result of industrial activity (Latham and Boutin 2015). Some forests, such as urban forests and plantations (monocultures), receive more and different use by humans than natural forests located further from urban and peri-urban areas.

Little is known about the relative susceptibility of different forest types to mammal invasions, but predictions can be made based on invasion theory. Elton (1958) predicted that species-rich communities (e.g., intact tropical continental rainforest) may be more resistant to invasion than those that are species poor (e.g., forested oceanic islands). Plantations and/or forests impacted by humans may be more prone to being invaded because of the higher availability of niches for invading organisms (di Castri 1989) and linear features that can be used as movement corridors by invading mammals (Latham and Boutin 2015). Urban forests are often the first sites for invasions because they are close to people that accidentally or intentionally liberate individuals of an introduced species, i.e., high propagule pressure (Liebhold et al. 1995). Urban areas can support high densities of invasive species like feral and pet cats (*Felis catus*) (Calhoun and Haspel 1989) and rodents (Tamayo-Uria et al. 2014), with potential for spill-over impacts on nearby forest. Although not strictly invasive, pet cats and dogs (*Canis lupus familiaris*) can be included as nonindigenous populations of mammals that have ‘invaded’ many urban forests (e.g., Loss et al. 2013). Human food subsidies enable pet cats and dogs to occur at significantly higher densities than wild counterparts, potentially leading to higher negative impacts on indigenous prey. Further analyses of historical introductions and establishments of mammals in different forest-types may shed light on these predictions.

A range of ecological and economic impacts

Direct and indirect ecological impacts

A direct or an indirect ecological impact consists of any significant change in an ecological pattern or process (Pyšek et al. 2012). Stakeholders perceive the impacts of invasive populations as being good or bad, and evaluate them based on their ecological, economic, and sociological impacts (Simberloff et al. 2013). Often there is general consensus among stakeholders about an invasive population and its impacts. For example, most people accept that accidentally introduced commensals such as rats and mice have significant unwanted impacts and consequently they are almost universally considered pests (Veitch and Clout 2001). Conversely, species that were intentionally introduced as a resource to be harvested by sportspeople and/or commercial operators—e.g., fur-bearing animals and game species—are often the subject of divisive perceptions amongst stakeholders (Nugent and Fraser 1993).

There are myriad examples of the direct ecological impacts that populations of nonindigenous mammals have had on forests. Numerous species of mammalian herbivores have been introduced around the world (Long 2003), with many becoming invasive and impacting native vegetation in forests (Wardle et al. 2001; Novillo and Ojeda 2008). Browsing and grazing by introduced ungulates like deer and feral goats can significantly reduce abundances of preferred species of plants and change the composition of forests such that they become dominated by the least palatable plant species (Nugent et al. 2001; Wardle et al. 2001; Campbell and Donlan 2005). Even at very low densities deer can prevent regeneration of highly palatable plants, but generally, low, relatively stable post-irruption densities have less effect on regeneration. For example, current low densities of red deer in mountain beech (*Fuscospora cliffortioides*) forests in New Zealand were found to impact forests slightly, but at levels unlikely to prevent canopy replacement (Bellingham et al. 2016b). Conversely, introduced North American beaver are deforesting large tracts of *Nothofagus* forest in southern South America and currently occur at densities sufficiently high to prevent local-scale regeneration (Novillo and Ojeda 2008; Fig. 1).



Fig. 1 Invasive mammalian herbivores can impact native vegetation in forests, reducing abundances of preferred species of plants and ultimately changing plant species composition in forests, sometimes radically. For example, North American beavers (*Castor canadensis*), were introduced to Tierra del Fuego, Argentina, c. 70 years ago, from where they spread into neighboring Chile. Beaver foraging, and lodge and dam building has deforested large tracts of *Nothofagus* (southern beech) forest and, in some areas, beavers have prevented local-scale regeneration of forest. Beaver-killed beech trees can provide short-term positive effects for some indigenous species, such as Magellanic woodpeckers (*Campephilus magellanicus*), by increasing foraging opportunities; however, this is predicted to diminish over time through loss of old growth forest (Crego et al. 2016). This photo of a lake on Navarino Island, southern Chile, shows dead beech trees (killed by beaver gnawing) from the shoreline to mid-slope, resulting in an altered ecosystem state dominated by grasses and forbs. Photo credit: Bob Webster

It can be difficult to disentangle the direct impacts of one invasive herbivore on native vegetation if it occurs sympatrically with other introduced or native herbivores (Forsyth et al. 2000). In Argentina, invasive mammals from the families Cervidae (deer), Suidae (pigs), and Leporidae (rabbits and hares) often occur sympatrically with a suite of ecologically equivalent native species, with diet overlap between at least some of the nonindigenous and indigenous species (Novillo and Ojeda 2008). Similarly, diet overlap existed between introduced hog deer (*Axis porcinus*) and native swamp wallabies (*Wallabia bicolor*) in shrub-encroached coastal grassy woodland in Victoria, Australia (Davis et al. 2008). Measurements of vegetation responses in exclosures variously excluding one or more sympatric herbivores can help disentangle specific impacts. For example, where both introduced red deer and tamar wallaby (*Macropus eugenii*) had been excluded from New Zealand forest,

plant species diversity increased by 142%, whereas if only wallabies were excluded the increase was 57% (Warburton 2005). The implication is that deer, at the density assessed, are probably a greater threat to native vegetation than wallabies, but to ameliorate all impacts, both species need to be removed. An indigenous herbivore occurring sympatrically with an introduced herbivore might also need to be managed to ameliorate a direct impact on native vegetation, particularly if land-use changes or some other global driver of change has caused the indigenous herbivore to become overabundant (Putman and Moore 1998; Côté et al. 2004; Davis et al. 2008). Alternatively, an introduced herbivore may competitively exclude one or more indigenous ones (e.g., Mack et al. 2000; Vázquez 2002; Hemami et al. 2005), thus management intervention may ameliorate unwanted impacts to both indigenous vegetation and mammals.

Introduced herbivores can also indirectly impact other animal taxa and forest ecosystem processes, e.g., below-ground microbes and invertebrates (Wardle et al. 2001; Wardle and Bardgett 2004; Allombert et al. 2005) and forest birds (Martin et al. 2010). Introduced ungulates in New Zealand cause community- and ecosystem-level effects by reducing browse layer plant diversity (Wardle et al. 2001). In turn, this can result in altered diversity in the litter layer and consequently, populations of many groups of litter-dwelling mesofauna and macrofauna can also be adversely affected (Wardle et al. 2001). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) introduced to the archipelago of Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada, reduced the abundance and diversity of plant species, which, in turn, simplified understory invertebrate and shrub-dependent songbird communities compared with islands not impacted by deer (Martin et al. 2010). In New Zealand, selective browsing by invasive brushtail possums results in higher biomass of the nitrogen-fixing tree *Carmichaelia odorata*, with strong flow-on effects on primary succession in forests (Bellingham et al. 2016a). Rooting by feral pigs alters soil nitrate levels, species richness of native seedlings and saplings, and tree species composition in temperate New Zealand rainforests (Krull et al. 2013). Introduced mammalian herbivores may also directly and indirectly affect carbon sequestration in forests, with the greatest impacts predicted to occur when herbivory

increases canopy disturbance and disrupts subsequent recovery of tree species (Peltzer et al. 2010).

Introduced mammalian predators are one of the most pervasive drivers of global change, particularly on islands where they have devastated indigenous prey populations (Lowe et al. 2000; Blackburn et al. 2004; Russell et al. 2015; Woinarski et al. 2015). Globally, the most problematic invasive predators comprise carnivores—domestic (feral) cat, Javan (small Indian) mongoose, red fox (*Vulpes vulpes*), and stoat (short-tailed weasel, *Mustela erminea*)—and opportunistic omnivores (some of which are primarily herbivorous)—brushtail possum, house mouse, black rat, Norway rat, long-tailed macaque (*Macaca fascicularis*), and feral pig (Lowe et al. 2000). All these invasive predators occur in forest ecosystems and all have negatively impacted indigenous prey in the areas to which they have been introduced.

The direct impacts of these introduced predator species have been well-documented. For example, Medina et al. (2011) showed that feral cats on islands have contributed to 33 (13.9%) of 238 global bird, mammal, and reptile extinctions; cat impacts on prey were considered moderate in c. 70% of cases and high in c. 30%. Introduced feral and free-ranging domestic cats have also significantly impacted native prey on mainland, even on continents that have native Felidae (Loss et al. 2013). Invasive black, Norway, and Polynesian rats eat seeds and inflorescences, endangering indigenous palatable plants (Townsend et al. 2006; Meyer and Butaud 2009). They are notorious for having had widespread impacts on invertebrates, reptiles and birds, and are among the largest contributors to seabird extinction and endangerment worldwide (Townsend et al. 2006; Jones et al. 2008; Fig. 2). Similarly, house mice, despite their diminutive size, are also known to have significant impacts on indigenous plants, invertebrates, and landbirds and seabirds, especially where they occur in the absence of (usually) invasive mammalian predators that suppress mouse densities (Angel et al. 2009).

The effects of invasive mammals can be complex and indirect, affecting not only populations, but also community composition and ecosystem properties through trophic cascades (Simberloff et al. 2013). For example, rats introduced from Europe to forested offshore islands in New Zealand prey on seabird eggs and chicks and severely reduce bird densities (Townsend et al. 2006). Islands with seabird densities reduced by



Fig. 2 Mammalian predators have caused the extinction or endangerment of indigenous prey in many ecosystems—particularly islands—to which they have been introduced. For example, invasive rodents, including black (ship) rats (*Rattus rattus*; pictured), have had widespread impacts on indigenous invertebrates, reptiles and birds. This photo shows a black rat killing a New Zealand fantail (*Rhipidura fuliginosa*) in forest, North Island, New Zealand. Photo credit: Nga Manu Images Copyright

rat predation had significantly reduced forest soil fertility compared with islands unaffected by rat predation (Fukami et al. 2006). Disrupted sea-to-land nutrient transport by seabirds had wide-ranging cascading effects on belowground organisms and the ecosystem processes they drive (Fukami et al. 2006; Wardle et al. 2009). Ironically, invasive populations of some rodents have had positive impacts by replacing indigenous species in ecosystem processes or as a resource for remaining indigenous species (Simberloff et al. 2013). For example, invasive rats perform some pollination functions of New Zealand birds that they helped to eliminate (Pattimore and Wilcove 2012). Similarly, invasive black rats and green anoles (*Anolis carolinensis*) have become important prey (50 and 33% of 156 recorded prey items, respectively) for the Ogasawara buzzard (*Buteo buteo toyoishimai*) on the Ogasawara Islands, Japan, following the decline of indigenous prey (Kato and Suzuki 2005; Fig. 3).

Economic impacts

A detailed discussion on the economic costs of impacts caused by invasive forest mammals is beyond the scope of this ecologically focused review, but it is worth highlighting a few points. Economic impacts caused by nonindigenous invasive species can be divided into damage to productive and environmental assets, and the costs of controlling invasives to

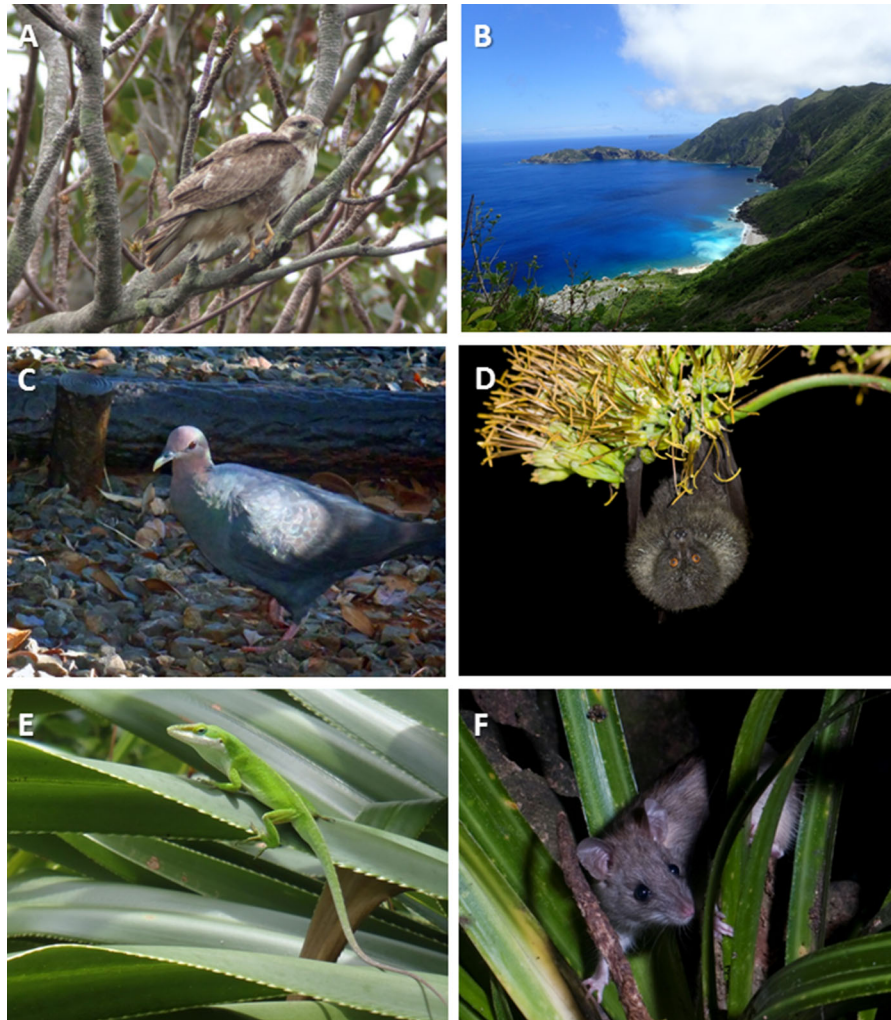


Fig. 3 The effects of invasive mammals in forests can be complex and indirect, affecting not only populations, but also community composition. For example, the diet of Ogasawara buzzards (*Buteo buteo toyoshimai*; **a**) on the Ogasawara Islands (**b**), Japan, historically comprised indigenous prey like the red-headed woodpigeon (*Columba janthina nitens*; **c**) and Bonin flying fox (*Pteropus pselaphon*; **d**). The pigeons declined following predation by introduced feral cats (*Felis silvestris catus*) and flying foxes declined as a result of habitat

mitigate unwanted impacts (Mack et al. 2000; Hone 2007). We do not discuss the direct costs associated with controlling populations of invasive mammals, as these have been well documented (e.g., Parkes and Murphy 2003; Russell et al. 2015; Holmes et al. 2016).

Damage to productive assets, such as crops and plantation forests, has been estimated for some invasive populations of forest mammals. For example, feral pigs cause environmental damage in forest

disturbance. Ironically, the buzzards now largely depend on two introduced vertebrates, invasive green anoles (*Anolis carolinensis*; **e**) and black rats (*Rattus rattus*; **f**), for food (Kato and Suzuki 2005). Black rats and green anoles both have unwanted impacts on indigenous plants and animals, but controlling them to mitigate these impacts concurrently reduces food availability for buzzards. Photo credits: Atle Olsen (**a**), Naho Mitani (**b**, **c**, **e**), Yushi Osawa (**d**), and Nga Manu Images Copyright (**f**)

patches where they live, but can also have significant impacts on crops and farmland adjacent to vegetated refugia (Choquenot et al. 1996; Pimental et al. 2005; Hone 2007). Pimental et al. (2005) estimated that the total annual costs associated with damage caused by feral pigs in the United States in the early-2000s were US\$800 million (equivalent to c. US\$984 million in 2016 values). Feral pigs have similarly been estimated to cause significant agricultural damage in Australia,

estimated at >US\$75.5 million p.a. (equivalent to c. US\$126 million p.a. in 2016 values) (Choquenot et al. 1996). Damage has been estimated for some other populations of introduced mammals that dwell at least partly in forests, but generally there is a lack of robust information on these costs at national and especially global levels (Mack et al. 2000).

Information about the loss in potential economic output for non-market values in forest ecosystems, such as natural capital and ecosystem services, is scarce or non-existent (Costanza et al. 1997). Latham et al. (2016) estimated the economic value of the impacts to relevant ecosystem services of two invasive species of forest-/scrub-living wallabies (*Macropus* spp.) introduced into New Zealand from Australia. They found that uncertainty about the values placed on ecosystem services and the difficulty in disentangling the impacts of sympatric introduced herbivores resulted in imprecise estimates. Nevertheless, the analysis showed overwhelmingly that the costs of these invasive wallabies to ecosystem services were high, with a net benefit from controlling them to mitigate unwanted impacts.

Interactions with other global drivers of change

There is increasing recognition that the impacts of invasive species need to be considered in tandem with other drivers of global environmental change (Felton et al. 2009), such as climate change (Van der Putten et al. 2010; Walther 2010) and land-use change (Mantyka-Pringle et al. 2012). Climate change is likely to affect species' distributions and abundance (Root et al. 2003) and community composition (McMahon et al. 2009), as well as processes such as nitrogen deposition (Larsen et al. 2011), flowering and fruiting phenology of plants (McEwan et al. 2011), and plant–pollinator relationships (Schweiger et al. 2010). Taken together, the impacts of invasive species and climate change in ecosystems are likely to be significant and multifaceted (Mainka and Howard 2010; Winder et al. 2011). Thus, understanding their interactive effects is vital for the conservation and management of biodiversity and ecosystem function in forest ecosystems (Walther et al. 2009).

What are the synergistic impacts of invasive species and climate change on trophic processes in forest ecosystems? There is currently limited evidence for

such impacts. On Montserrat, British West Indies, control of feral livestock (primarily goats and feral pigs) prevents climate-induced invasion by feral guava (*Psidium guajava*) and Java plum (*Syzygium cumini*) (Peh et al. 2015), thereby increasing the value of ecosystem services provided by a tropical forested ecosystem. In New Zealand, succession from shrublands to forest ecosystems is curtailed by a combination of seed predation by introduced mammals and an altered fire regime caused by climatic shifts and increasing temperatures (Perry et al. 2015).

Evidence for exacerbated trophic-level impacts by invasive mammals in forest ecosystems as a result of changes in climate is also limited. In New Zealand beech forests, multi-annual beech seed masting (strongly variable seed production by a geographically definable population of plants; Kelly et al. 2008) drives a highly irruptive invasive mammal community (Holland et al. 2015). Masting events are driven by climate, specifically, a change in mean summer temperature from one year to the next which spans the crucial period of pollination and flowering (Kelly et al. 2013). An increasing frequency of such episodes is predicted with high confidence for New Zealand over the coming decades (Kelly et al. 2013). Mast events represent a pulsed food resource for invasive mammals (Ruscoe and Pech 2010). Tompkins et al. (2013) showed through predictive modelling that an increased frequency of mast events would result in an increased biomass of invasive rodents in these forest ecosystems, with potential impacts on native fauna through predation and competition for food resources (Innes et al. 2010; Ruscoe et al. 2011), and on vegetation through both herbivory (Gormley et al. 2012) and reduced ecosystem services such as pollination and seed dispersal (Anderson et al. 2011).

Synergistic effects of land-use change and invasive species may operate to impact on forest ecosystems in two ways. Certainly, the global impacts of forest fragmentation are significant, with 70% of the world's remaining forests being within 1 km of forest edge (Haddad et al. 2015). First, fragmentation of forests might facilitate invasion by introduced mammals, which has been demonstrated in forest fragments in east Africa (Byrom et al. 2015) and in Asia (Gibson et al. 2013). Invasive mammals can reach high densities in adjacent modified or matrix habitats, which in turn has major impacts on forest community structure and function (Didham et al. 2007), and can

also impede forest regeneration (Fleury et al. 2015). Alternatively, reforestation might provide habitat for invasive mammals, facilitating movement among patches (Abdelkrim et al. 2010), or increasing genetic connectivity (Etherington et al. 2014).

Challenges of managing mammalian invaders in forests

Strategies and tactical options for managing invasive mammals are well established (e.g., Braysher 1993; Parkes 1993; Bomford and O'Brien 1995; Parkes and Murphy 2003). The two positive strategic options to manage pest mammals are a one-off management action that provides a permanent benefit (eradication or some forms of biological control) or a management action that must be sustained in perpetuity to achieve a benefit (e.g., sustained or repeated control or exclusion fencing) (Parkes and Murphy 2003). A third option is to 'do-nothing'; perhaps because the impact is not considered high enough priority or because there is insufficient funding for management.

Eradication is a favoured strategy for many populations of invasive mammals, but it makes sense as a policy only if it is achievable (Parkes and Panetta 2009). It is also not suitable for invasive mammals that are being managed for their resource value as well as to mitigate their unwanted impacts. For example, various species of deer have been introduced to a number of countries around the world for hunting, but they also have unwanted impacts on native vegetation (Nugent and Fraser 1993). In some instances, it may be possible to manage them for both values depending on the nature of the pest–asset–impact relationship. The extent of pest damage is related to pest abundance, the availability of the asset being damaged, and the relationship between pest damage and pest density can take a linear or curvilinear form (Hone 2007; Norbury et al. 2015). The presence of a threshold indicating zero (or low) damage at low to moderate pest-density means not all pests need to be removed to prevent damage (Hone 2007).

Constraints on managing invasive forest mammals

The extent of the global spread and impacts of nonindigenous species discussed in this paper has led to a progressive replacement of biodiversity with

biosimilarity (Vitousek et al. 1996; Warren 2007). This is largely a result of humans either intentionally translocating species because of their utilitarian value (e.g., fur, meat, recreation, pet keeping, and transport) or unintentionally as a consequence of travel and trade (e.g., commensal rodents) (Bonanno 2016). The diversity of reasons and support for initial introductions (i.e., the value humans place on different species) often remain strong even when an introduced species becomes invasive and clearly has significant negative impacts on indigenous flora and fauna. For example, brushtail possums introduced into New Zealand from Australia to establish a fur trade (Warburton et al. 2000) have significant impacts on forest health (Gormley et al. 2012) and livestock health (Warburton and Livingstone 2015), but the fur harvesting industry persists and is currently growing because of increasing demand for possum-fur products. Consequently, managing invasive mammals is often a complex problem—it must take into account scientific information, but also consider moral arguments (what we ought to do) and political arguments (what is appropriate to do) (Dickman et al. 2015). Developing policy and management plans for managing invasive mammals involves considering a plethora of views reflecting moral differences, value judgements, cultural differences, and ethical and animal welfare concerns. We consider each of these in turn.

The ecological impacts of invasive species on indigenous biodiversity vary widely but are undeniable; however, how these impacts are viewed and managed is a value judgement that extends beyond the science of invasion biology (Sagoff 2005; Callicott 2013). Managers of invasive mammals need to substantiate what the impact of the invasive population is and whether that impact is 'bad' (i.e., there is a broad acceptance that the impact is judged unacceptable). Scientists and managers have to be careful not to commit the naturalistic fallacy of believing what is 'natural' is good and what is 'not natural' is bad, i.e., not everyone shares the view invasive mammals are bad (Brown and Sax 2005; also see Cassey et al. 2005). For example, several deer species were introduced into New Zealand for hunting; they are now found in most forests, resulting in significant modification of understorey vegetation (Nugent et al. 2001). Whether or not this is categorized as bad may depend on whether a person is a conservationist who believes any modification of the natural environment is bad, a hunter who

values the deer as a resource more than the cost of any impacts on flora, or someone who might be undecided because there is uncertainty as to whether deer partially fulfil the herbivory role that the now extinct large ratites (moa birds; Order: Dinornithiformes) provided (see different perspectives in Caughley 1983; Forsyth et al. 2010; Steer 2016). So it is important to recognize that not all introduced invasive populations are automatically pests—some are resources, at least in some areas and to some people.

Alternative views of managing invasive mammals come not only from philosophical considerations, but also from different cultural perspectives. For example, North American beaver introduced to Tierra del Fuego, Argentina, are ecosystem engineers and their engineering has significantly modified landscapes by felling riparian trees, building dams and flooding low lying areas (Haider and Jax 2007; Fig. 1). Interviews of local stakeholders identified that some regarded the beavers as “belonging to us” and attributed to them a “settler’s spirit”—that is, a “new neighbour” that has emigrated in search of new habitats, adapting themselves to their new harsh environment “like us” (Schüttler et al. 2011). In contrast to accepting an invasive species as “belonging to us” after an arbitrary time period, Carthey and Banks (2012) used their assessment of responses of indigenous bandicoots (marsupial prey) to domestic dogs, and by inference to dingoes (*Canis lupus dingo*; predator introduced 4000 years ago) in Australia, to suggest an introduced species should be considered a ‘native species’ when impacted indigenous species lose their naivety to the invasive. This highlights the contrast between what people and their culture might tolerate, and what science might tell us about whether the ongoing presence of an invasive species is ecologically acceptable or not. Using Buddhist and Taoist ceremonial releases of nonindigenous species as “good deeds”, as an example, Dickman et al. (2015) contend, based on moral relativism, that conservation biologists have a duty to promote good science, even if that requires implicitly or explicitly criticizing a cultural practice.

Even within societal groups attitudes and responses to official management intervention may vary. As an example, 258 new ungulate populations were recorded in New Zealand between 1993 and 1996, with 26% of these resulting from illegal releases, presumably to increase hunting opportunities (Fraser et al. 2000).

Similarly, feral pigs are a popular game species in the USA. Initially released as a hunting resource in Texas, accidental and intentional releases and natural spread have resulted in them invading 32 US states and four Canadian provinces (Denkhaus and Tuttle 2006). Such a dichotomy of values makes achieving any management goal, especially eradication, a risky undertaking, and even initial discussions of possible eradication may provoke retaliatory releases (Beaven 2008). For example, Ford-Thompson et al. (2015) investigated public attitudes towards an invasive population of Javan (rusa) deer (*Rusa timorensis*) in the Royal National Park, Sydney, Australia. They reported that the key themes that were most divisive were whether deer should remain in the park, the heritage value of deer, the need to remove deer, and the need to kill nonindigenous species. Once identified, potential causes of conflict can be used to help develop management plans that at least acknowledge and may account for the wide range of public attitudes.

Tactical options for controlling invasive populations of mammals support the application of a wide range of tools including non-lethal and lethal options (Bomford and O’Brien 1990; Byrom et al. 2016). Current control tools, especially toxins used for controlling small mammals have both non-target (Hoare and Hare 2006; Thompson et al. 2014) and welfare impacts (Mason and Littin 2003). Secondary (non-target) poisoning of invasive species can produce positive outcomes, e.g., invasive mustelids dying after consuming poisoned rodents in New Zealand (Murphy et al. 1998) or negative outcomes, e.g., the indigenous fisher (*Martes pennanti*) dying after consuming poisoned rodents in California, USA (Thompson et al. 2014). Even when the outcome is ecologically beneficial, interest groups who oppose the use of toxins in control programs may focus on negative aspects such as animal welfare or perceived environmental risks. Large species such as deer, feral pigs, feral horses (*Equus ferus caballus*), and goats are most often controlled using either ground-based or aerial shooting (Bayne et al. 2000). All lethal methods have welfare costs ranging from some slow-acting toxins such as anticoagulants that have significant welfare impacts (Mason and Littin 2003) to quick acting toxins, kill traps, and shooting that have fewer welfare impacts (Warburton et al. 2008; Hampton et al. 2015a). Non-lethal options are not exempt and their welfare impacts also need to be assessed (Hampton et al. 2015b), and

the outcomes of their use measured. Animal welfare frameworks have been developed that allow managers to choose control tools based on their humaneness (e.g., Littin et al. 2014).

Animal welfare and animal rights groups can have a significant influence on planned invasive species management programs, occasionally resulting in lengthy delays and loss of opportunities for effectively managing an invasive species, especially achieving eradication. For example, a plan to eradicate invasive eastern grey squirrels from Italy was challenged by animal rights groups and resulted in legal proceedings and a subsequent lengthy judicial review. Although the National Wildlife Institute (the Italian government agency for wildlife research and conservation) was acquitted, the 3 year delay resulted in a significant expansion of the grey squirrel's range and the decision that eradication was no longer achievable (Bertolino and Genovesi 2003; Perry and Perry 2008). Such opposition must be met with well-reasoned and robust planning, and several authors have suggested frameworks to ensure pest control programs are justified (e.g., Littin et al. 2004). These include a set of principles as follows:

1. The aim of each control program must be clear and justified.
2. The harms of each program must also be made clear.
3. Control must only be undertaken if the aims can be achieved.
4. The methods selected must be the most humane (and economically achievable).
5. The outcomes of each control program must be assessed, and
6. Once the desired aims have been achieved, steps must be taken to maintain the beneficial state.

Additionally, when the proposed management intervention has a high level of uncertainty, Warburton and Norton (2009) suggest that control programs are structured as adaptive management programs, so even if they fail to produce predicted outcomes, the manager can learn and improve future actions. Wildlife managers also need to acknowledge and consider the multiple values of stakeholders, including both those that relate to ecological processes, species and populations, and those related to individual animal welfare, professional duty, scientific integrity, and public welfare (Minteer and Collins 2008). They

suggest this intersection of ecological science and community values could be best addressed within the emerging field of ecological ethics.

Knowledge gaps and future directions

Achieving effective management of populations of mammals invasive in forests will require many knowledge gaps to be filled across research disciplines including, ecology, biology, economics, genomics, social science, public policy, and philosophy. The knowledge gaps can be grouped under four main headings:

1. *Understanding impacts on forest ecosystems* In many ecosystems, including forests, there is a poor understanding of what the long-term impact of an invasive species will be and, if eradication is not an option, what the relationships are between the invasive species' density and its impacts on a range of taxa and ecosystem processes. In addition, research is required on changes in forest ecosystems after invasive species are suppressed or eradicated. In some cases, especially in highly impacted areas, these may be effectively novel ecosystems.
2. *Global change and invasive mammals* A better understanding of the synergistic impacts of invasive species in tandem with each other and with other drivers of global environmental change will also be vital. Knowledge gaps 1 and 2 need to be filled by improved knowledge of the ecological, economic, and social aspects of particular invasives at specific sites.
3. *Strategic options and tactical solutions for managing invasives* There are essentially three strategic options for managing invasives: (1) eradicate, (2) suppress to a level such that their impacts are acceptable, and (3) do nothing. In some cases, these options may not be mutually exclusive: for example, 'local' eradication of an invasive species can be the objective in high impact areas but suppression or no intervention may be the only feasible options elsewhere. Deciding which strategic approach to choose is well documented, but as new technologies are developed (e.g., gene drives; Esvelt et al. 2014) those choices might change. Development of new,

highly effective technologies has the potential to change how and where invasive species might be managed.

4. *Social licence to operate* In most countries, invasive species cannot be managed without the support of affected communities, interest groups, political processes, and policy/regulatory hurdles. How best to manage such public discourse is well documented (e.g., Allen et al. 2001, 2014; McLeod et al. 2015). For example, if new genomic technologies are to be developed, there is an urgent need to determine if such technologies will be acceptable and what social demands might constrain their specifications and use.

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