Biol Invasions (2017) 19:1353–1378
DOI 10.1007/s10530-016-1367-z

ELTON REVIEW 2

Plant invasion science in protected areas: progress and priorities

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Received: 2 November 2016 / Accepted: 30 December 2016 / Published online: 25 January 2017

Abstract Invasive alien species are a major problem for managers of protected areas (PAs) worldwide. Until the 1980s biological invasions were widely considered to be largely confined to anthropogenically disturbed sites and the widespread disruption of ecosystems in PAs by invasive species was not globally perceived as a major threat. A working group of the SCOPE program on biological invasions in the 1980s showed that PAs are not spared from major disruptive effects of invasions. Early research focused on descriptive studies of the extent to which PAs were invaded. More recent research explored drivers of invasion, and in the last decade much work has focused on understanding the impacts of invasions. We review the current understanding of alien plant invasions in PAs, focusing on four themes: (1) the status and macroecological patterns of alien plant invasions; (2) the threats that invasive alien plants (IAPs) pose and the impacts detected to date; (3) the current focus of invasion science in PAs; and (4) research priorities for advancing science-based management and policy. Of a sample of 59 widespread IAP species from a representative sample of 135 PAs globally, trees make up the largest proportion (32%), followed by perennial herbs (17%) and shrubs (15%). About 1857 papers have been published on alien species in PAs; 45% have focused on alien plants. Some textbook examples of impacts by IAPs originate from PAs, illustrating the severe threat to the core function of PAs. Impacts have been quantified at the species and community levels through the displacement and alteration of habitats. In some cases, native

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species abundance, diversity and estimated species richness have been altered, but reversed following control. At an ecosystem level, invasive plants have radically altered fire regimes in several PAs, in some cases causing regime shifts and transforming woodlands or savannas to grasslands. Invasions have also had a major impact on nutrient cycles. Protected areas are performing an increasingly important part of the global response to stem the rate of environmental change. Despite this, integrated efforts involving science, management and policy that are sufficiently resourced to generate insights on the status and dynamics of IAPs in PAs are insufficient or even lacking. Such efforts are needed to pave the way for monitoring trends, revising legislation and policies, and improving management interventions to reduce the extent and magnitude of impacts of invasive plants in PAs. While policy instruments to support management of non-native species date back to the 1930s, there has been a substantial increase in legislative support and general awareness since the early 2000s. Still, opportunities to improve research for PAs need to be created. Towards this goal, the establishment of a global PA research network could provide a unique vehicle to explore questions across species or functional groups and systems, at a scale currently beyond existing abilities. Developing an integrated global database with standardized, quantitative information could form part of such a networks function.

Keywords Biological invasions · Conservation · Impact · Model system · Nature reserves

Introduction

An increasingly complex mixture of anthropogenic factors is driving the loss of global biodiversity and is impeding the functioning of ecosystems and their capacity to deliver essential services. Protected areas (PAs) are a key component of the global response to environmental change and degradation (Hannah et al. 2007; Gaston et al. 2008; Conroy et al. 2011). Despite many problems with effectiveness of reserve design, governance and other aspects (Terborgh 1999; Pressey et al. 2015), PAs are contributing positively to biodiversity conservation (Leverington et al. 2010). However, despite the increasing attention given to conservation inside and outside PAs in many parts of the world, biodiversity continues to decline (Butchart et al. 2010). Some drivers of global change and biodiversity loss may be managed to some extent inside PAs and in buffer zones around them (e.g. habitat fragmentation and transformation due to agriculture, forestry and urbanization; Koh and Gardner 2010; Foxcroft et al. 2011a). However, other drivers cannot be as effectively mitigated by formally protecting land. One such driver that directly threatens biodiversity, even within the most effectively managed PAs, is the invasion of alien species, and invasive alien plants (IAPs) are a major concern in this regard (Foxcroft et al. 2013a).

Few PAs are effectively isolated from surrounding landscapes. Most are embedded in a mosaic of land-use types, the spatial configuration of which can form a network of potential sources of and pathways for alien species (e.g. Foxcroft et al. 2007; Meiners and Pickett 2013). In areas with minimal human presence, key natural processes may remain more or less intact whereas in human-dominated landscapes many natural processes are disrupted or altered to various extents. In many cases, such disruptions create windows of opportunity for the establishment and proliferation of invasive species. Although there have been many studies of IAPs in PAs, most are largely descriptive assessments of the extent of invasion, while many other aspects of invasions remain poorly explored. For plants, a global assessment showed that 37% of 282 quantitative studies on impacts of invasive species in the peer-reviewed literature originated from work in PAs. However, they suffer from marked geographical biases: much more work has been done in the Americas and on Pacific Islands than in Africa, Asia and Europe (Hulme et al. 2014). There are also concerns among managers that past research on IAPs in PAs has focused too heavily on the basic ecology of the invading species, rather than exploring management issues (e.g. Andreu et al. 2009).

This review aims to move beyond case studies to assess what we know of alien plant invasions in PAs and how such knowledge has influenced our capacity to manage these invasions. We structure our discussion around four broad questions: (1) How many invasive species are there? (2) What harm do they do? (3) Is research directed appropriately to improve our understanding of the problem? (4) Do we know enough to be able to manage the problem? We address these under the following headings:

I. History and present status of plant invasions in PAs worldwide
   a. Historical milestones regarding knowledge of plant invasions in PAs
   b. Invasive plants in PAs around the world: numbers and patterns
   c. Major invasive plant species in PAs
II. What threats do invasive alien plants pose to PAs?
   a. Are impacts of invasive plants in PAs sufficiently well studied?
   b. Species- and community-level impacts
   c. Ecosystem-level impacts
III. What invasion science has been done in PAs?
   a. Contribution of research conducted in PAs to invasion ecology
   b. Protected areas as model systems for invasion ecology
IV. Priorities for research on alien plant invasions in PAs
   a. Establish a working group to coordinate research on plant invasions in PAs
   b. Develop standardized quantitative information on levels of invasion and protocols for monitoring
   c. Science and management in PAs need to respond to different socio-political contexts

History and present status of plants invasions in protected areas worldwide

Historical milestones regarding knowledge of plant invasions in protected areas

Concern over the presence of alien species in PAs has been expressed for over 150 years. One of the earliest examples comes from 1864, when concerns were raised about European weeds invading the Yosemite Valley State Park in California (Randall 2011) (Table 1). In 1921 the American Association for the Advancement of Science (AAAS) opposed the introduction of alien plants and animals into national parks in the United States (Shelford 1926) and in the 1930s US National Park scientists expressed concerns over the presence of alien species (Houston and Schreiner 1995). The British Ecological Society (British Ecological Society 1944) and Board of Trustees for National Parks in South Africa (Bigalke 1947) later echoed these sentiments.

The last major international research program to focus specifically on invasive alien species (all taxa) in PAs was a working group on invasions in nature reserves, initiated under the SCOPE (Scientific Committee on Problems of the Environment, hereafter "SCOPE") program on biological invasions in the 1980s (Wildlife Conservation and the Invasion of Nature Reserves by Introduced Species: a Global Perspective; Macdonald et al. 1989). Results from this work appeared in six papers in a special issue of *Biological Conservation* that addressed invasions in PAs on islands (Brockie et al. 1988), on arid lands (Loope et al. 1988), in tropical savannas and dry woodlands (Macdonald and Frame 1988) and in Mediterranean-type climate regions (Macdonald et al. 1988). Usher (1988) synthesized the results and provided some generalizations. One of the main interests of the nature reserves subprogram of SCOPE was to examine differences in invasibility between disturbed and undisturbed habitats (inside and outside PAs). Until then, it was widely accepted that invasions were problematic only in disturbed sites. The SCOPE subprogram aimed to answer the same three specific questions that were the focus of SCOPE overall, but specifically for PAs: (1) What factors determine whether a species will be an invader or not? (2) What site properties determine whether the level of an ecosystem's susceptibility to invasion? (3) How should information from questions 1 and 2 be used to manage invaded ecosystems?

SCOPE led to major advances in the understanding of plant invasion dynamics. It also highlighted the importance of studying invasions in PAs. For example, Usher (1988) concluded: "Protected areas collectively constitute a useful sample of the world's ecosystems. They also provide ideal outdoor laboratories". SCOPE showed that the nature and degree of invasions differed substantially between PAs in different parts of the world (see "Invasive plants in protected areas around the world: numbers and patterns" section). However, the key finding to emerge from the 24 case studies was that alien plants are present in all nature reserves, except those in Antarctica (Usher 1988). Only the specially protected areas of the maritime Antarctic had no records of introduced species in the 1980s (Usher

Table 1 Time line of milestone publications, important events, and policy documents that paved the way for the current state of knowledge and research on plant invasions in protected areas. The highly cited articles illustrate the importance being placed on research emanating from work in protected areas. Only articles with more than 40 citations (as of May 2016) were considered highly cited. The full reference for the highly cited articles is provided in the reference list

Year	Highly cited articles and number of citations	Conventions and policy
1864		Concerns raised in Yosemite National Park
1921		Concerns raised by US National Park Service
1930		Concerns raised by AAAS
1933		African Convention Nature & Natural Resources
1944		Concerns raised by British Ecological Society
1982		1980s SCOPE Programme on Invasions in Nature Reserves
1990	Cuddihy and Stone (1990) [128]	
1991	Aplet et al. (1991) [47]	
1992	Cole et al. (1992) [202]	
1993	Cowie and Werner (1993) [54]	
1994	Lonsdale and Lane (1994) [116]	IUCN ISSG Founded
1996	Randall (1996) [104]	
1997	Lombard et al. (1997) [76]	1997–2010 GISP Programme
1998	Horton and Neufeld (1998) [90]	
1999	Stohlgren et al. (1999) [207]	
2000	Magura et al. (2000) [90]	
2001	Evans et al. (2001) [233]	
2002	Pyšek et al. (2002) [149]	CBD: 6th Conference of the Parties
2003	Knick et al. (2003) [160]	IUCN Vth World Parks Congress & Bern Convention
2004	Pauchard and Alaback (2004) [190]	
2005	Tabarelli et al. (2005) [134]	
2006	Sheppard et al. (2006) [125]	
2007	Wilson et al. (2007) [141]	
2008	Bargagli (2008) [97]	Convention on Biological Diversity Article 8(h)
2009	Cadotte et al. (2009) [54]	
2010	Pickering et al. (2010) [59]	CBD: 10th Conference of the Parties
2011	Hulme (2011) [44]	
2012		IUCN World Conservation Congress
2013		Bern Convention
2014		IUCN World Park Congress

and Edwards 1986). This contrasts with the current situation, three decades later, when over 250 alien plants are established across the Southern Ocean islands (Shaw 2013). Outside of Antarctica, Macdonald et al. (1989) provided many examples to illustrate many types of impacts of alien plants on ecosystem structure and functioning. A recommendation from the SCOPE subprogram was that alien plants in PAs that threaten endemic species with extinction and/or have strong impacts at a landscape scale should be given priority attention (Usher 1988). Another finding was that tourism is an important driver of invasions in PAs: a positive relationship between the numbers of tourists and the number of alien species in PAs was demonstrated (Usher 1988; Macdonald et al. 1989).

Concerns about the potential impacts of invasive alien species (all taxa) in PAs arose in parallel with the initiation of various regional conventions and agreements (Shine et al. 2005) (Table 2). While the intention of these agreements and target regions vary

Table 2 A sample of global approaches and policy support for managing invasive alien species in protected areas (for a comprehensive list of international and regional instruments in recent decades, see Shine et al. 2000)

Convention	Date and provisions	Aim/excerpt
African Convention on the Conservation of Nature and Natural Resources	1933: Article 7(5)	To "give consideration to the desirability of preventing the introduction of exotic trees or plants into national parks or reserves"
ASEAN Agreement on the Conservation of Nature and Natural Resources	1985: Article 3(3c)	Contracting parties shall "…endeavour to regulate and, where necessary, prohibit the introduction of exotic species"
Convention for the Conservation of the Biodiversity and the Protection of Wilderness Areas in Central America	1992: Article 24	Parties agree that mechanisms shall be established for the control or eradication of all exotic species which threaten ecosystems, habitats and wild species
CBD: 6th Conference of the Parties	2002: Decision (VI/23)	"Guiding principles for the prevention, introduction and mitigation of impacts of alien species that threaten ecosystems, habitats or species"
IUCN Vth World Parks Congress	2003	States that "management of invasive alien species is a priority issue and must be mainstreamed into all aspects of protected area management. The wider audience of protected area managers, stakeholders and governments needs urgently to be made aware of the serious implications for biodiversity, protected area conservation and livelihoods that result from lack of recognition of the IAS problem and failure to address it. Promoting awareness of solutions to the IAS problem and ensuring capacity to implement effective, ecosystem-based methods must be integrated into protected area management programmes. In addition to the consideration of benefits beyond boundaries, the impacts flowing into both marine and terrestrial protected areas from external sources must be addressed"
Bern Convention	2003: Article 11 (2.b) European Strategy on Invasive Alien Species	Contracting Parties undertake to strictly control the introduction of non-native species. Further, to draw up national strategies to control the problem in protected areas, and to improve their capacity in terms of awareness raising, monitoring and management of the problem
Convention on Biological Diversity (CBD)	2008: Article 8(h)	"Each contracting Party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species"
10th COP Ramsar Convention on Wetlands	2008: Resolution X.1	Highlights invasive alien species as one the "challenges that still require urgent attention in order to achieve wetland wise use under the Convention"

Table 2 continued

Convention	Date and provisions	Aim/excerpt
CBD: 10th Conference of the Parties	2010: Decision X/31 on "Protected areas"	"..invites Parties to consider the role of invasive alien species management as a cost effective tool for the restoration and maintenance of protected areas and the ecosystem services they provide, and thus to include management of invasive alien species in the action plans for implementation of the programme of work on protected areas"
11th COP Ramsar Convention on Wetlands	2012: Resolution XI.3 STRATEGY 1.9 Invasive alien species	Encourage Contracting Parties to develop a national inventory of invasive alien species that currently and/or potentially impact the ecological character of wetlands, especially Ramsar Sites, and ensure mutual supportiveness between the national inventory and IUCN's Global Register of Introduced and Invasive Species (GRIIS); develop guidance and promote procedures and actions to prevent, control or eradicate such species in wetland systems
IUCN Invasive Species Specialist Group	2012: Policy brief on biological invasions included in the IUCN documentation for the "Rio+20 - United Nations Conference on Sustainable Development"	Identified specific actions on the issue for 2012–2020, including awareness raising, eradication in key areas of the most harmful invasive species, and incorporating invasive species in water and land-use planning at all scales from local to global, including in protected areas
IUCN World Conservation Congress	2012: Resolution 21	Calls on all countries to promote eradication campaigns of priority invasive alien species, … giving priority to key areas such as protected areas, and requesting the Director General and IUCN Commissions to promote the compilation and dissemination of best practice guidelines on invasive alien species management in protected areas, promote appropriate training to address this threat and enhance more effective management in protected areas, and also calling funding agencies to support prevention, eradication and control campaigns, especially in protected areas
Bern Convention	2013: Recommendation No. 167 on European Guidelines on Protected Areas and Invasive Alien Species	European Guidelines on Protected Areas and Invasive Alien Species Formally adopted by the Standing Committee of the Bern Convention in 2013, recommending that Contracting Parties (1) where necessary, draw up national strategies to control invasive alien species in protected areas, in particular where endangered native flora and/or fauna may be at risk from such alien species; taking into account in that context of the European Guidelines on Protected Areas and Invasive Alien Species mentioned above; (2) instruct managers of protected areas and other appropriate

Table 2 continued

Convention	Date and provisions	Aim/excerpt
		conservation staff to collaborate in the tasks involved in communication and awareness raising, monitoring, prevention and management of invasive alien species, making sure that management plans take due account of the need to deal with invasive alien species in protected areas; (3) consult, when possible and as appropriate, the actors involved in management and conservation of protected areas, as well as scientific bodies, on the identification of priority IAS in protected areas and in the preparation and the implementation of mandatory measures to tackle these priority IAS in protected areas; (4) keep the Standing Committee informed of measures taken to implement this recommendation
IUCN World Park Congress IUCN SSC Invasive Species Specialist Group and the Secretariat of the Convention on Biological Diversity	2014: sessions on the problems of invasive species in protected areas Promise of Sydney, Stream 1 of the WPC, "Achieving Conservation Goals", includes Recommendation 16	The Promise of Sydney vision ensures that protected areas worldwide will strive to eliminate activities and policies that result in the introduction and spread of invasive species. The topic of biological invasions was discussed in Stream 1 of the WPC, "Achieving Conservation Goals", the outcomes of which includes Recommendation 16, calling on governments, the global and local communities, and protected areas to urgently address the rising threats to biodiversity from invasive species
12th COP Ramsar Convention on Wetlands	2015: Resolution XII.2 The Ramsar Strategic Plan 2016–2024	Urges all Contracting Parties and invites other stakeholders to take on the renewed challenge of implementing the Strategic Plan through its goals and targets, that include: Target 4: Invasive alien species and pathways of introduction and expansion are identified and prioritized, priority invasive alien species are controlled or eradicated, and management responses are prepared and implemented to prevent their introduction and establishment. And requests Parties to develop inventories of invasive alien species, to enforce policies and guidelines on the issue, and to monitor the effectiveness of wetland invasive alien species control programmes

widely in these documents, many apply specifically to PAs. Early examples include the African Convention on the Conservation of Nature and Natural resources (1968), the Bern Convention on the Conservation of European Wildlife and Natural resources (1979) and the ASEAN Agreement on the Conservation of Nature and Natural Resources (1985). SCOPE probably had some influence on additional agreements, for example on the drafting of the Protocol for the Implementation of the Convention on the Conservation of Nature in the South Pacific (1990), the Convention for the Conservation of the Biodiversity and the Protection of Wilderness Areas in Central America (1992) and the Alpine Convention in the Field of Nature Protection and Landscape Conservation (1994). The Standing Committee to the Bern Convention has played a particularly active role on the topic of alien species invasions, first through a series of targeted recommendations, in 2003 through the adoption of the comprehensive European Strategy on Invasive Alien Species (Genovesi and Shine 2004), and more recently through the development of a series of Codes of Conduct to reduce the impacts of invasions due to various human activities (e.g. Brundu and Richardson 2016).

Although records of alien plant species started appearing in general floras as early as the 1700s (Chew and Hamilton 2011), systematic scientific interest in IAPs in PAs was initiated by the SCOPE subprogram on nature reserves in the 1980s. Since then this research has been supported by well-cited and influential publications that, together with other key information sources, have been canalized into political conventions and agreements (Table 1) and provided foundations of current perspectives and understanding of biological invasions in PAs.

Invasive plants in protected areas around the world: numbers and patterns

The global evidence base on the level of plant invasions in PAs is sparse and there is no comprehensive global database on which to build a rigorous analysis of macroecological patterns (Foxcroft et al. 2013a). Nonetheless, the data allow for large regions or countries to assess trends over the last 30 years since plant invasions in PA have become a focus of research interest (Usher 1988).

Several studies have found that PAs contain fewer IAPs than their surroundings and that they act to some extent as barriers against colonization by alien plants. In his pioneering study of alien floras in 184 regions all over the world, Lonsdale (1999) found that PAs harbored about half the number of alien plants compared to non-protected areas, and that the main driver of increasing the levels of invasions was the numbers of visitors. Similarly, across 302 nature reserves declared between 1838 and 1996 in the Czech Republic, reserves were found to contain significantly fewer alien species than non-protected areas. Their numbers, as a percentage of the total reserve floras, decreased towards colder environments at higher altitudes and were highest in regions with the highest human populations (Pyšek et al. 2002). Another analysis of the same Czech data set revealed that over the period indicated above, nature reserves accumulated alien plant species significantly more slowly than surrounding non-protected landscapes, suggesting that the (semi)natural vegetation in temperate PAs, together with avoidance of human-induced disturbances, creates a filter against invading aliens (Pyšek et al. 2003). A similar conclusion—that the presence of intact natural vegetation slows the establishment of alien plants—was made in a study that examined the role of the boundary of South Africa's Kruger National Park, South Africa, as a filter to alien plants. In areas where there was more than 90% natural vegetation within a 5 km radius of the park, alien plants were significantly less common (Foxcroft et al. 2011a; Jarošík et al. 2011).

The above mentioned principle is not universally valid. In fact, it can be assumed that there are very few, if any, PAs in the world that are completely free of alien plants (Foxcroft et al. 2013a), and it is now clear that alien plants can invade natural areas that have not experienced anthropogenic disturbances, such as the Gros Morne NP in boreal Canada (Rose and Hermanutz 2004).

However, we lack systematically sampled data on the current levels of plant invasions in PAs worldwide; the last comprehensive global data were collected within the SCOPE program in 1980s (Fig. 1). These studies tallied 1874 invasive alien vascular plant species in the 24 nature reserves assessed in the 1980s (Usher 1988; Macdonald et al. 1989). Although the proportional contribution of alien plants to total floras varied widely, some generalizations can be made. In the 1980s, PAs most heavily affected by invasions were on islands, including tropical islands where floras comprised between 31 and 66% alien species. Reserves in mainland tropical and arid subtropical areas were generally less invaded; alien species in arid regions of the United States and Africa accounted for 4–10% of floras. Protected areas in temperate regions of the northern hemisphere mostly had more alien plant species than those in the southern hemisphere (Fig. 1). Twenty years later, a Global Invasive Species

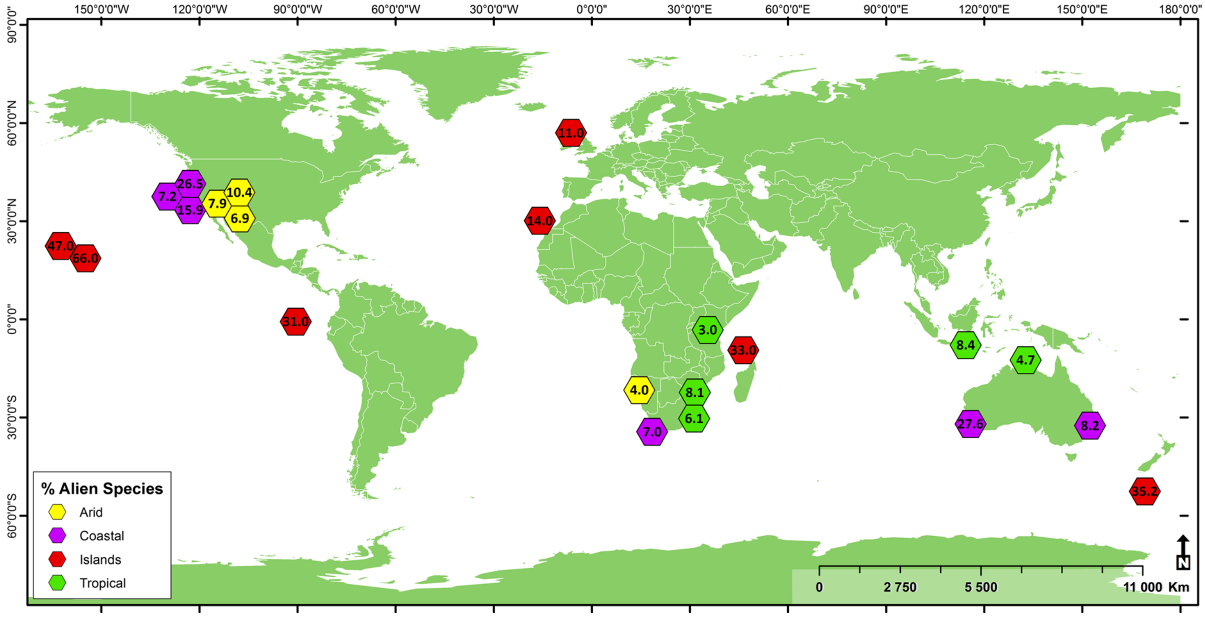

Fig. 1 The extent of plant invasions in 24 protected areas, based on data from the SCOPE program on nature reserves (Usher 1988, map based on Kučera and Pyšek 1997). The numbers are percentages of alien species in the total flora of the protected area. The following reserves are displayed: Islands: Rhum/Rum (Scotland)—11%, Selvagem Grande (Portugal)—14%, Campbell (New Zealand)—35.2%, Galápagos (Ecuador)—31%, Aldabra (Seychelles)—33%, Maui—47%, Hawai'i Volcanoes—66%. Tropical: Ngorongoro (Tanzania)—3%, Kruger National Park (South Africa)—8.1%, Hluhluwe (South Africa)—6.1%, Baluran (Java)—8.4%, Kakadu National Park (Australia)—4.7%. Coastal: Sequoia National Park, Mt Whitney and Kings Canyon (California)—7.2%, Pinnacles National Monument (California)—15.9%, Jasper Ridge (California)—26.5%, Myall Lakes (Australia)—8.2%, Kings Park (Australia)—27.6%, Cape of Good Hope (South Africa)—7%. Arid: Skeleton Coast (Namibia)—4%, Organ Pipe Cactus (Arizona)—6.9%, Death Valley (California)—7.9%, Canyonland and Arches (Utah)—10.4%. The *symbols* are used to distinguish between island (*red*), tropical (*green*), coastal (*purple*) and arid (*Yellow*) reserves

Program (GISP) report identified 487 PAs where noxious IAPs were recorded and represented a threat to biodiversity (De Poorter 2007).

On a continental scale, repeated assessments over time are available from the USA. These indicate that in North America the problem is accelerating. As early as 1980, a report to the US Congress stated that 300 National Park Service areas perceived alien plants and animals as a threat to natural resources (Houston and Schreiner 1995). In the 1990s, at least 115 invasive alien plant species were identified in PAs in Virginia alone (Heffernan 1998). Site-specific management plans have detailed the resources needed to control IAPs in more than 145 national parks in the USA (Drees 2003). The most comprehensive study to date estimated that 20,305 alien plant "infestations" by 3756 unique species covered 7.3 million ha in 218 national parks in the USA (Allen et al. 2009).

One reflection of the situation described above is that invasive plants are almost unequivocally regarded as a threat by managers. In a 2009 survey The Nature Conservancy (TNC) reported that about 60% of 974 of their projects around the world considered IAPs to be the main threat (Randall 2012). In US national parks, 61% of 246 park managers indicated that alien plant invasions were moderate or major concerns (Randall 2011). In southern Africa, in the 1980s, only seven out of 307 PA managers that responded to a survey were of the opinion that no alien species were known to occur in their reserve (Macdonald 1986). An assessment of 110 PAs in South Africa's KwaZulu-Natal province concluded that IAPs were the greatest threat to biodiversity in the province (Goodman 2003). In Europe, a 2012 survey showed that managers of PAs perceived IAPs as the second greatest threat to their areas after direct habitat loss (Pyšek et al. 2013). A recent survey by TNC showed that almost all TNC managers considered alien species to cause ecological or aesthetic impacts and that if additional resources were available they would increase control efforts (Kuebbing and Simberloff 2015).

Major invasive plant species in protected areas

No systematic quantitative overview of invasive alien species causing problems in PAs is available at global, international and/or regional levels (De Poorter 2007). Better information is available at the site and national levels, but the lack of standardized criteria for listing species precludes an accurate global picture. The global assessment by De Poorter (2007) listed 37 significant invasive plant species for Europe, 84 for USA and Canada, 57 for Australia and New Zealand, 47 for Africa, 30 for Asia, 13 for Oceania, 10 for South and Central America and Mexico, based on the criterion of having impacts causing, for example, a reduction in native biodiversity, ecosystem change or habitat alteration (Table 5.1 in De Poorter 2007).

For a new perspective we used the recent global overview of plant invasions in PAs in the recent book *Plant invasions in protected areas: patterns, problems and challenges* (Foxcroft et al. 2013a) which gives insights from a representative sample of the world's PAs. The chapter authors, experts from their regions, discussed several of the most severe IAP problems that PAs in the region are faced with. Although no standard metric was applied in the chapters for ranking the order of importance of IAPs in different PAs, we included all species repeatedly mentioned as being problematic in the book. This resulted in a list of 59 species that is a representative sample of the most widespread, best-studied and most influential invasive plant species in PAs around the world (Table 3). Based on the information from regional experts and from our own experience in many PAs worldwide, this represents a good checklist of 59 of the "worst invasive plants in protected areas of the world". The best represented life forms on the list are trees (19 species, 32%), perennial herbs (10 species, 17%) and shrubs (9 species, 15%). Other life forms are less frequent: grasses (7 species, 12%), aquatic plants including one fern and one alga (5 species, 8%), vines (4 species, 7%) and annual/biennial herbs and succulents (3 species each, 5%). In terms of taxonomy, large species-rich families are best represented, but only Fabaceae (8 species), Poaceae (7), Asteraceae (5) and Myrtaceae (4) are represented by more than two species; the remaining 29 families are each represented by one or two species.

Some species in Table 3 are very widespread invaders that have large global distributions: *Poa annua* (reported as naturalized from 269 regions out of the total of 843 regions included in GloNAF global database; van Kleunen et al. 2015), *Arundo donax* (220), *Melia azedarach* (204), *Eichhornia crassipes* (202), *Lantana camara* (197), *Rumex acetosella* (188), *Psidium guajava* (165), *Robinia pseudoacacia* (154), *Pistia stratiotes* (148), *Leucanthemum vulgare* (141), and *Opuntia ficus-indica* (139) are all invasive across at least 15% of the globe (Table 3). Not all the major invaders in PAs (Table 3) have large global distributions and some (e.g. *Merremia peltata*, *Lygodium microphyllum* and *Maesopsis eminii*) have quite restricted invasive ranges and effective management is still a feasible option. Thirty-eight percent of the 59 IAPs in PAs are naturalized in less than 5% of global regions (Fig. 2) possibly due to their narrower optimal environmental requirements. However they are still highly invasive and cause severe impacts across the range where they have invaded (e.g. *L. microphyllum* in the Florida Everglades).

The European list of De Poorter (2007) includes 25 trees and shrubs, eight perennials, and four annuals. However, for this continent we also have a more detailed picture of how the major invasive plants are distributed in PAs from a survey in which managers were asked to list species they considered most harmful in areas under their control. Among the 378 taxa listed at least once, the top IAP were knotweeds (*Fallopia japonica*, *F. sachalinensis* and *F.* × *bohemica*) which were reported for 41% of PAs, *Impatiens glandulifera* (25%), *Robinia pseudoacacia* (22%), *Ailanthus altissima* (14%), *Heracleum mantegazzianum* (9%) and *Ambrosia artemisiifolia* (9%)(Pyšek et al. 2013). Interestingly, a number of species perceived as the top invaders at the site level in European PAs are not listed for this continent in the global survey for Europe reported by De Poorter (2007), but some appear on the list of the most invasive plants in PAs globally (Table 3).

What threats do invasive alien plants pose to protected areas?

Are impacts of invasive plants in protected areas sufficiently well studied?

Understanding and quantifying impacts caused by IAPs is crucial for directing and prioritizing interventions to

Table 3 A sample of 59 alien plant species that are reported as invaders from 135 protected areas from around the world in Foxcroft et al. (2013a). For their global distribution, expressed as the number of regions in the GloNAF database (n = 843; van Kleunen et al. 2015) in which the species is reported as naturalized (see Fig. 2)

Species	Family	Life form	# Regions naturalized
Acacia mearnsii	Fabaceae	Tree	49
Acacia saligna	Fabaceae	Tree	39
Ailanthus altissima	Simaroubaceae	Tree	119
Alliaria petiolata	Brassicaceae	Biennial herb	50
Ammophila arenaria	Poaceae	Grass	35
Anredera cordifolia	Basellaceae	Vine	76
Arundo donax	Poaceae	Grass	220
Brachiaria mutica (syn. *Urochloa mutica*)	Poaceae	Grass	98
Caesalpinia decapetala	Fabaceae	Shrub	44
Carpobrotus edulis	Aizoaceae	Succulent shrub	48
Caulerpa taxifolia	Caulerpaceae	Aquatic alga	n.a.
Cedrela odorata	Meliaceae	Tree	24
Cerastium fontanum	Caryophyllaceae	Perennial herb	80
Chromolaena odorata	Asteraceae	Shrub	76
Chrysanthemoides monilifera	Asteraceae	Perennial herb	31
Cinchona pubescens	Rubiaceae	Tree	14
Cinnamomum verum	Lauraceae	Tree	49
Clidemia hirta	Melastomataceae	Shrub	41
Cortaderia selloana	Poaceae	Grass	66
Cytisus scoparius	Fabaceae	Shrub	90
Eichhornia crassipes	Pontederiaceae	Free-floating aquatic plant	202
Fallopia japonica	Polygonaceae	Perennial herb	98
Gunnera tinctoria	Gunneraceae	Perennial herb	12
Hakea sericea	Proteaceae	Shrub	9
Hedychium gardnerianum	Zingiberaceae	Perennial herb	23
Hydrilla verticillata	Hydrocharitaceae	Submerged aquatic plant	53
Hymenachne amplexicaulis	Poaceae	Grass	11
Hypericum perforatum	Hypericaceae	Perennial herb	104
Impatiens glandulifera	Balsaminaceae	Annual herb	74
Lantana camara	Verbenaceae	Shrub	197
Leucanthemum vulgare	Asteraceae	Perennial herb	141
Leycesteria formosa	Caprifoliaceae	Shrub	18
Lygodium microphyllum	Lygodiaceae	Vine	1
Maesopsis eminii	Rhamnaceae	Tree	1
Melaleuca quinquenervia	Myrtaceae	Tree	24
Melia azedarach	Meliaceae	Tree	204
Melinis minutiflora	Poaceae	Grass	88
Merremia peltata	Convolvulaceae	Vine	8
Miconia calvescens	Melastomataceae	Tree	16
Mikania micrantha	Asteraceae	Vine	36
Mimosa pigra	Fabaceae	Tree	40
Opuntia ficus-indica	Cactaceae	Submerged aquatic plant	139
Opuntia stricta	Cactaceae	Submerged aquatic plant	84

Table 3 continued

Species	Family	Life form	# Regions naturalized
Parthenium hysterophorus	Asteraceae	Annual herb	119
Pistia stratiotes	Araceae	Free-floating aquatic plant	148
Poa annua	Poaceae	Grass	269
Prosopis juliflora	Fabaceae	Tree	71
Prunus serotina	Rosaceae	Tree	33
Psidium cattleianum	Myrtaceae	Tree	62
Psidium guajava	Myrtaceae	Tree	165
Rhododendron ponticum	Ericaceae	Shrub	15
Robinia pseudoacacia	Fabaceae	Tree	154
Rubus niveus	Rosaceae	Shrub	19
Rumex acetosella	Polygonaceae	Perennial herb	188
Sagina procumbens	Caryophyllaceae	Perennial herb	98
Salvinia molesta	Salviniaceae	Free-floating aquatic plant	n.a.
Spathodea campanulata	Bignoniaceae	Tree	67
Syzygium jambos	Myrtaceae	Tree	86
Ulex europaeus	Fabaceae	Shrub	121

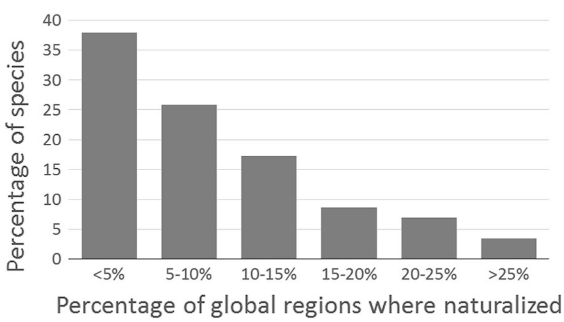

Fig. 2 Global naturalization success of species that have been reported as invasive species causing problems in protected areas over the world (Foxcroft et al. 2013a; see Table 3). The graph is a frequency distribution of the percentage from the regions included in the GloNAF database (n = 843; van Kleunen et al. 2015) from which species listed as invaders in PAs are reported as naturalized. Note that the figure does not relate specifically to PAs, rather it indicates how successful a species is as an invader globally

focus on those taxa that are most likely to cause serious harm (Hulme et al. 2014). Despite the strong recent trend in invasion biology towards studying the impacts of IAPs in a more objective way (e.g. Vilà et al. 2011; Pyšek et al. 2012; Simberloff et al. 2013; Blackburn et al. 2014; Bellard et al. 2016; Downey and Richardson 2016), the scientific capacity to accurately quantify and predict impacts is still lacking, although progress is being made on this front (Blackburn et al. 2014; Hawkins et al. 2015; Kumschick et al. 2015). A key challenge lies in agreeing on appropriate metrics for quantifying impacts. For example, in PAs—as with many regional or global assessments of threats to biodiversity—attention is often given mainly or exclusively to factors that threaten elements of biodiversity with extinction, the focus being on the endpoint of processes along an extinction trajectory, rather than other thresholds and processes that cause an attrition of biodiversity (Downey and Richardson 2016). Another challenge is to account for context-dependency to be able to disentangle the complex interactions between species traits and habitat features (Pyšek et al. 2012; Kueffer et al. 2013b) and the multiple spatial and temporal scales at which these interactions operate (Kumschick et al. 2015). Kueffer et al. (2013b) suggest that studying an invasion at only one site might allow for spurious conclusions. This may be alleviated by studying species within and outside PAs or across PAs, or across a gradient of abundances of alien plant invasions (Hulme et al. 2013). Although the population and community ecology of many plant invasions has been reasonably well studied, there is a poorer understanding of the interactions between them. Without a major advancement in understanding the interactions among IAPs on ecosystem function and dynamics, biogeochemistry and other system properties, little progress can be expected in improving management interventions (Strayer 2012).

A quantitative overview of 282 publications dealing with impacts of invasive plants worldwide revealed that 37% were conducted in PAs (Hulme et al. 2013). While it is difficult to judge whether this figure is high or low as there is no baseline against which to compare it, the geographic distribution of this research provides a clear signal—most studies on impacts in PAs have been conducted in North and South America, and far fewer in Africa, Asia and Europe (Hulme et al. 2013). This differs from a general picture of geographical biases in invasion ecology, where Europe and North America are significantly better studied than other regions (Pyšek et al. 2008). As the coverage by PAs on these two continents is very similar, with 14.4% of North America and 13.6% of Europe conserved (UNEP-WCMC 2014), the greater focus on PAs in North America compared to Europe seems to be attributable to researchers' preferences and societal needs, rather than indicating more opportunities due to larger areas invaded by plants in PAs in the former.

In the next section we draw on the approach used by Foxcroft et al. (2013a) as a framework for addressing negative impacts due to plant invasions that we consider most pertinent to PAs. These include impacts on species and communities; ecosystem properties; and biogeochemistry and ecosystem dynamics. Although these categories are not discrete and species interact across them, both as drivers and responders, they are a convenient approach for addressing the impacts in relation to the level of biological organization (Pyšek et al. 2012).

Species- and community-level impacts

For these kinds of impacts caused by invasive plants, strong direct competitive effects of IAPs over native plant species were frequently considered to be a primary mechanism and evidence to support this has been found in many studies (Levine et al. 2003). To quantify changes across landscapes following the introduction and invasion of alien plants, spiders or beetles have often been selected as indicators (McGeoch 1998). *Chromolaena odorata* invasion altered native spider assemblages, reducing the abundance, diversity and estimated species richness in Hluhluwe-iMfolozi Game Reserve in South Africa. These changes were, however, reversed immediately following clearing (Mgobozi et al. 2008). In a similar study in Kruger National Park, an assessment of the impact of *Opuntia stricta* found that across the gradient of the invader's abundance, beetle assemblages were significantly different, but beetle and spider species richness and species density, and spider assemblages, were not significantly altered by invasion density (Robertson et al. 2011).

Many case studies have focused on quantifying impacts on species of special conservation concern. Such cases, however, also illustrate broader habitat and ecosystem transformation. Stands of invasive *Chromolaena odorata* have displaced large and small mammals in Hluhluwe-iMfolozi Game Reserve (Dumalisile 2008). Megaherbivores are often threatened by invasion of their preferred grassland habitat, for example the vulnerable greater one-horned rhinoceros (*Rhinoceros unicornis*) in many of the PAs to which it is restricted. *Mimosa rubicaulis*, *M. diplotricha* and *Mikania micrantha* pose similar threats in Kaziranga National Park (India), while *Lantana camara*, *Ipomoea* spp., *Eupatorium* spp. and *Leea* spp. have invaded other reserves that are important for the greater one-horned rhinoceros (Talukdar et al. 2008). Nile crocodile (*Crocodylus niloticus*) nesting habitat and sex ratios may be altered due to shading, hence cooling of nests, by *Chromolaena odorata* which forms dense thickets on river banks (Leslie and Spotila 2001). Many species (e.g. *Mimosa pigra*, *Urochloa mutica*) impact wetland PAs that support an abundance of plant, fish and bird biodiversity and perform important functions. This is the case in the wetlands of Kakadu National Park in Australia, a Ramsar-listed site and a major tourist attraction (Setterfield et al. 2013).

Island systems have become icons of widespread invasions and habitat transformation. For example, about 80% of the total protected area of Hawaii Island now consists of degraded grasslands dominated by alien species, or sparsely to unvegetated volcanic terrain (Loope et al. 2013). Of the 415 endemic Hawaiian plant species assessed for the 2016 IUCN Red List (IUCN 2016), 87% are threatened with extinction. On Santa Cruz Island in the Galapagos National Park *Cinchona pubescens* has significantly reduced species diversity and the cover of most native species by at least 50%. Similarly, when *Rubus niveus* cover exceeded 60%, native species richness was reduced by 56%, with herbs being more affected than ferns. The abundance of almost all species was significantly reduced in heavily invaded sites (Gardener et al. 2013).

Hybridization and the loss of genetically distinct species have been underappreciated as a conservation concern (Rhymer and Simberloff 1996) compared to the physical disappearance of an entire species (Ehrlich 1988). Relatively recent objectives of biodiversity conservation stipulate that PAs should strive to protect populations of wild relatives of domesticated or cultivated species (Barber et al. 2004) and to isolate rare species from cross-compatible congeners (Mooney and Cleland 2001).

Ecosystem-level impacts

Much published information on ecosystem-level impacts of IAPs deals with fire regimes. Changes to fire regimes attributed to IAPs have significantly affected the structure of plant communities in many PAs and in some cases have transformed entire ecosystems to alternate stable states (Brooks et al. 2004; Alba et al. 2015). Vegetation in grasslands, savannas and various shrublands is fire-adapted and requires fire to sustain key ecosystem processes. However, human activities have also introduced fire to ecosystems where it is not a regular natural feature; in many areas this has caused substantial degradation. Changed fire regimes (in terms of frequency, intensity, timing and vertical positioning) due to invasive alien plants, often in concert with other drivers of change, is one of the most severe types of impacts associated with plant invasions in PAs. Maintaining natural processes in a naturally fire-prone system and managing fire in systems where it is not a regular occurrence provides substantial challenges to managers of PAs worldwide.

Introduced grasses that are fire-adapted and which invade areas where fire is not a regular feature recover quickly after being burned, often creating a positive feedback cycle that favors further invasion (D'Antonio and Vitousek 1992; Gaertner et al. 2014). For example, in Wildman Reserve in northern Australia, invasion of *Andropogon gayanus* increased fuels loads by up to seven times and fire intensity by up to eight times (Rossiter et al. 2003). In Dinosaur National Park and Snake River Birds of Prey National Park (USA) *Bromus tectorum* changed the fire frequency from one in 60–100 years, to one in 3–5 years, thereby transforming the native shrublands to an alternative state that is likely to be permanently dominated by alien grasses (Randall 2011). Over large areas of Everglades National Park, Big Cypress National Preserve and Arthur R. Marshall Loxahatchee National Wildlife Refuge, marshlands with sedges, grasses and herbs have been replaced by *Melaleuca quinquenervia* (Australian paper bark) which created dense stands of swamp forests with little or no herbaceous understory (Serbesoff-King 2003). *Melaleuca quinquenervia* promotes crown fires whereas the native plants have evolved with higher frequency, low intensity surface fires (Rundel et al. 2014). Another invasive plant that caused major changes to the natural fire regime in the Fakahatchee Strand State Preserve, Everglades National Park and Big Pine Key National Wildlife Refuge is *Lygodium microphyllum*. This vine-like fern climbs on trees and shrubs, forming thick mats which cause trees to collapse. Fires that would normally stop at the edge of native cypress sloughs travel up 'fire ladders' created by dry fronds of *L. microphyllum* to kill tree canopies (Schmitz et al. 1997). *Chromolaena odorata* also creates such fire ladders that substantially alter fire regimes in the savannas of eastern South Africa, resulting in large-scale mortality of native trees (Brooks et al. 2004). Loss of populations of species not adapted to fires can be rapid, posing a significant challenge to managers. In Saguaro National Park (south-western USA), 6 years after one fire fueled by the invasive grass *Pennisetum ciliare*, there was 24% mortality of the endemic saguaro cactus *Carnegiea gigantea* and 73% mortality of the native tree *Parkinsonia microphylla* (Esque et al. 2004). There are many other examples of invasive plant species triggering such regimes shifts in invaded ecosystems, many of them in protected areas (Gaertner et al. 2014).

Even fire-adapted native species are at risk in ecosystems where fire regimes have been transformed by IAPs. For example, in Table Mountain National Park in South Africa's fynbos region, Australian *Acacia* and *Hakea* species and *Pinus* species from Europe and North America are also fire-adapted species that persist and spread rapidly after fires (Richardson and Cowling 1992; Forsyth and van Wilgen 2008). These trees and shrubs increase biomass and radically alter fuel properties of the vegetation (van Wilgen and Richardson 1985), leading to increased fire intensity and erosion (van Wilgen and Scott 2001). Soil loss following fires in uninvaded fynbos typically amounts to 0.1 tons/ha whereas 6 tons/ha are lost following fires fueled by the high biomass in *Pinus*-invaded patches (Scott et al. 1998).

The overall impacts of ecosystem-level changes due to altered fire regimes such as those described above have not been assessed but have clearly been substantial and are growing in magnitude and complexity. Such impacts have greatly complicated management in affected PAs, frequently causing conflicts of interest between the requirements to maintain historical fire regimes to conserve species and communities, and diverting resources from other important conservation concerns.

For impacts on biogeochemistry and ecosystem functioning, including those on nutrient cycling and mineralization, the disruption of ecosystem function is driven by adding species traits to ecosystems. These include traits related to morphology, phenology and tissue chemistry and those that result in profound changes in biomass and productivity. In some cases long-term changes to ecosystem dynamics occur rapidly and lead to obvious and sometimes dramatic alterations of ecosystem functioning. The textbook example is the case of the nitrogen-fixing shrubs *Morella faya* and *M. cereifera* which increased soil nitrogen availability by up to 400% in Hawaii Volcanoes National Park. This triggered a cascade of changes by significantly altering plant succession trajectories and paving the way for many other major changes to the ecosystem, for example the increase in populations of alien earthworms. This in turn increased nitrogen burial rates, thereby further changing soil nutrient cycles (Vitousek et al. 1987; Vitousek and Walker 1989). Nitrogen-fixing Australian *Acacia* species have had similarly dramatic impacts over huge areas of fynbos vegetation in PAs in South Africa (e.g. Yelenik et al. 2004). In the Wildman Reserve in northern Australia, rapid and widespread invasion of the grass *Andropogon gayanus* inhibited soil nitrification, thereby depleting total soil nitrogen from the already nitrogen-poor soils (Rossiter-Rachor et al. 2009), leading to the transformation of diverse savanna ecosystems into dense grass monocultures. The examples cited above are the best-studied and most dramatic impacts, but long-term changes in ecosystem dynamics may also be more subtle and inconspicuous—even such subtle changes in plant-soil interactions may be steering many communities to irreversible alternative states (Vilà et al. 2011). More work is needed to examine fluxes and pools of nutrient cycles, including whole-site budgets, across multiple sites to gain a clearer understanding of such impacts (Ehrenfeld 2003).

However, with respect to the dramatic impacts that many species exert in PAs, it should be noted that there are many success stories as well (Simberloff et al. 2011). For example, 11 IAP species have been eradicated from Raoul Island Nature Reserve, New Zealand (Table 14.1 in West and Thompson 2013). In Florida Everglades National Park, invasive populations of *Melaleuca quinquenervia* have been reduced to about half of the originally invaded area (Center et al. 2012). However, such success stories are not well communicated and ways in which they can be made more accessible need to be developed.

What invasion science has been done in protected areas?

Contribution of research conducted in protected areas to invasion ecology

To determine how research on plant invasions in PAs has contributed to the knowledge and understanding of the field of plant invasions, we undertook a literature analysis (Fig. 3; "Appendix 1"). Between 1877 and 2015, a total of 59,525 papers were published on PAs and 38,447 on alien plant species in general. Among the PA studies were 1857 papers that dealt with alien species, of which 830 dealt with alien plants. Surprisingly, of all the papers that addressed alien plant species, only 2% were conducted in PAs. The region with the highest number of articles on alien plants in PAs is North America (330 studies), followed by Europe (244). While only 134 articles on alien plants in PAs are from Africa, their contribution to the number of all articles on alien plants in this continent was proportionally higher than the corresponding figure for North America. Of the 134 articles originating from Africa, 74% were from South Africa (Fig. 3). North America (with 14.9% of the global protected area network; UNEP-WCMC 2014) and Europe (12.9%) are over-represented in the literature on alien plants in PAs whereas Africa (13.8%) is underrepresented.

There has been a change in the focus of research on IAPs in PAs over time (Fig. 4). The analysis of similarities among articles published since 1969 onward

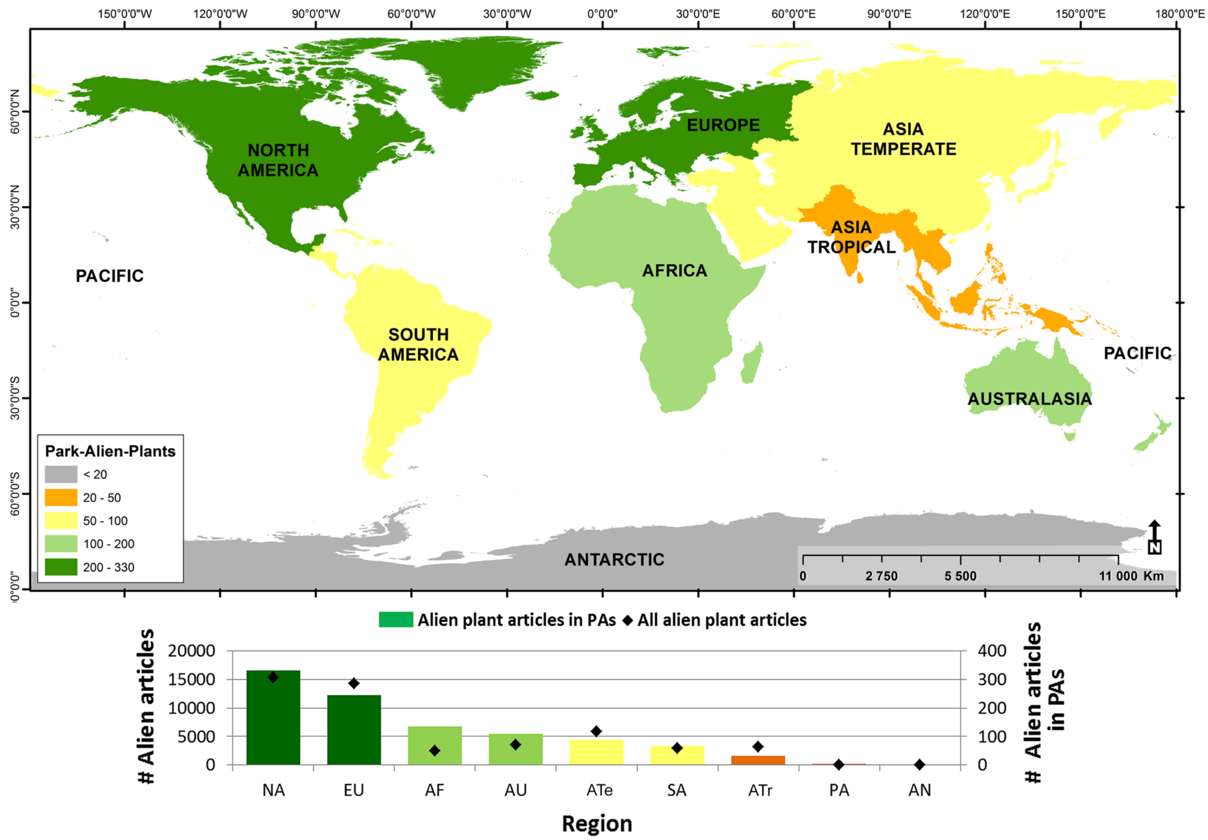

Fig. 3 The number of papers addressing alien plants in protected areas (*color scale*) per continent. The *bar graph* (bars colored by continent) shows the number papers in protected areas on alien plants compared to all articles dealing with alien plants in the literature regardless of where the study was done. The data were obtained by searching the SCOPUS database to extract papers published between 1877 and 2015 on (1) all alien biota, and alien plants in general; (2) all alien biota, and alien plants in PAs, using the search terms in the Supplementary material. The figure is based on 1857 papers that deal with alien species in PAs, of which 45% were on alien plants

showed that until the mid-1980s research addressed topics in a random fashion. A significant clustering in the focus of research is evident between 1986 and 1995. A structured and coordinated research effort (the SCOPE program) sought insights from PAs across a range of ecosystem types (see "Historical milestones regarding knowledge of plant invasions in protected areas" section). Several highly cited and influential articles were published during this period (Table 1).

To detect trends in specific research focus areas, six keywords were selected a priori and their frequency in papers since the 1970s was assessed (Fig. 5). The keywords (fire; impact; ecosystem; biodiversity; society; nutrient) were selected to include aspects related to ecosystems and ecosystem processes (fire, nutrients), impacts of alien plant invasions, biodiversity concerns and societal aspects. None of these keywords were highlighted between 1969 and 1981, indicating that other topics were more important foci of research at the time. Impacts of invasions dominated the studies conducted during the 1980s, largely due to activities associated with SCOPE. For example, Macdonald et al. (1989) assessed the manner in which IAPs could affect nature conservation. Interestingly, impact-related research only re-emerged as an important theme in PAs in the mid-2000s when impacts of IAPs became one of the central themes of invasion ecology in general (Pyšek and Richardson 2010). Studies on fire-related impacts of IAPs started in the early 1990s (D'Antonio 2000) and have become dominant since 2000. Studies on ecosystem properties have fluctuated in importance; they were unimportant in the late 1990s, but increased in importance after the mid-2000s and have remained important since then.

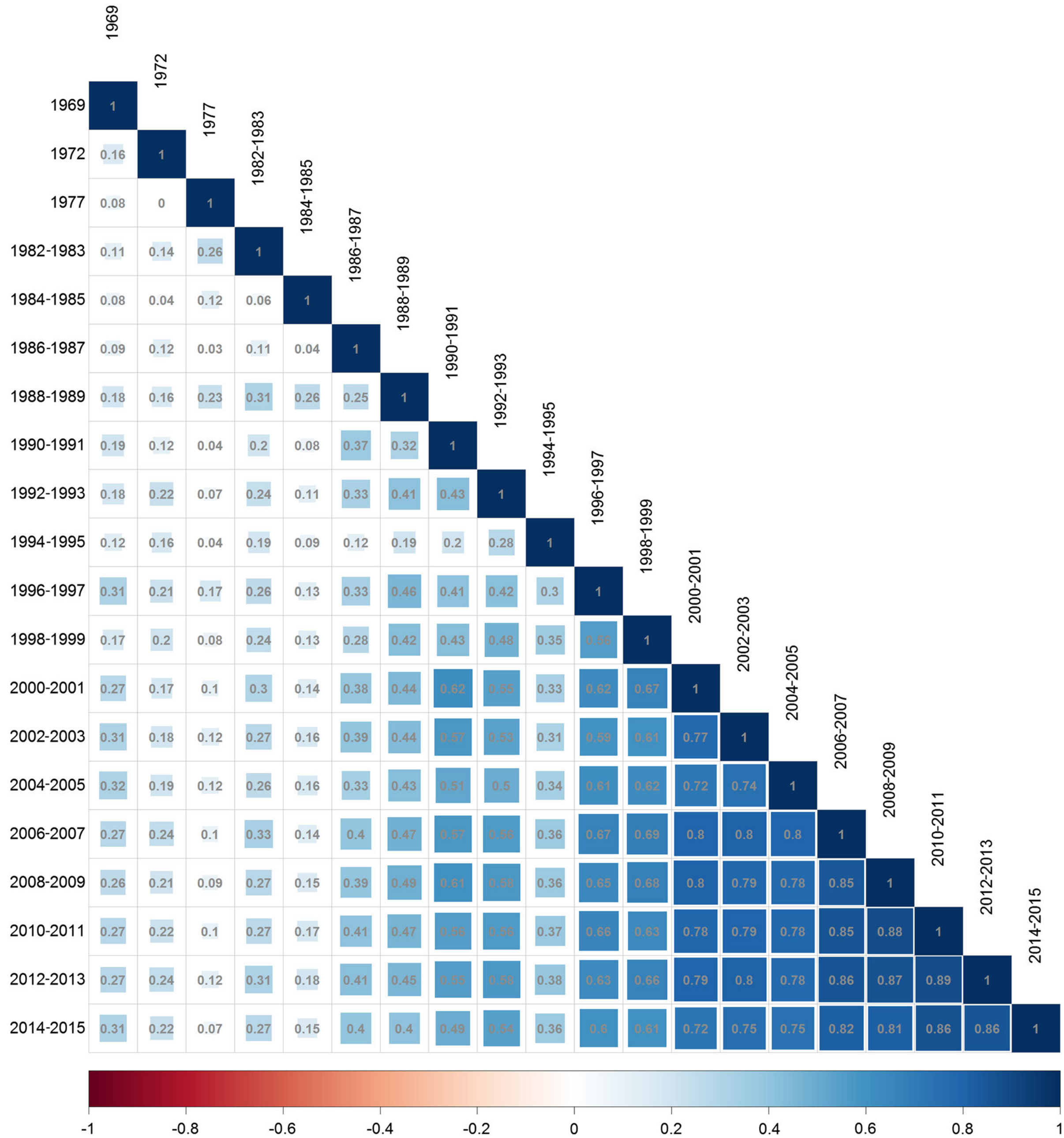

Fig. 4 Correlation matrix of keywords in articles in two-year periods, from 1969 to 2015. Values in the graph are Pearson product moment correlation coefficients. Values above 0.37 show the 2-year periods that are significantly correlated with each other based on the similarity between keywords, at a 95% confidence level. See "Appendix 2" for detailed description of the methods

Protected areas as model systems for invasion ecology

Many avenues of scientific enquiry related to a range of disciplines are being pursued in the quest for general theories in plant invasion science (Catford et al. 2009; Pyšek and Richardson 2010; Foxcroft et al. 2011b; Richardson 2011). Although specific mechanisms of invasion (such as those related to plant traits, features of the receiving environment, and context

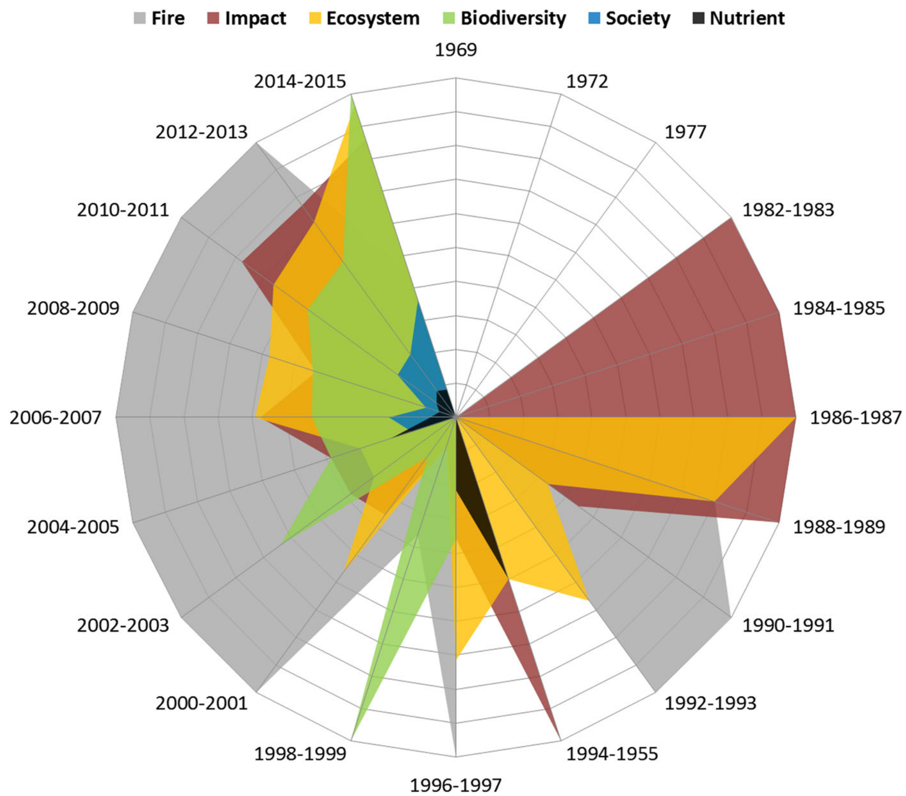

Fig. 5 Keywords selected a priori to determine trends in scientific themes in protected areas over time. The figure shows the numbers of times a word (*w*) in the legend is repeated per year (not number of papers in which words are quoted), rescaled by the maximum number of times all legend words (lw) are repeated (i.e. *w/max*(*lw*)). See "Appendix 2" for methods

dependency) have been explored in detail, much work remains to be done to integrate these insights to gain a robust predictive capacity. Kueffer et al. (2013b) proposed three approaches for integrating invasion science: (1) model system research; (2) multi-site studies; and (3) focused meta-analysis. Protected areas are well suited as research arenas for all three approaches.

Many PAs have a rich source of supporting information on biodiversity, environmental features and history. Many key aspects of ecological understanding have emerged from research in PAs (Martin et al. 2012) and some PAs have decade's worth of well synthesized information (e.g. Kruger and Serengeti in Africa; Kakadu in Australia; Bialowieza and Hohe Tauern in Europe; Yellowstone and Yosemite in the USA). Model systems should be conducive to addressing multiple research questions and be attractive to funders and collaborators. Many PAs qualify in this regard and have facilities such as laboratories, equipment and accommodation to support research efforts. The philosophy of adaptive management that is being widely applied in many PAs provides a rich source of information on success and failures for various management approaches (Roux and Foxcroft 2011). Different categories of PAs experience different levels of natural and anthropogenic disturbances; this provides a range of contexts within which to develop and test hypotheses, including the potential for studying gradients of protection and human use, from urban national parks to large wilderness areas.

Kumschick et al. (2015) advocate a range of parameters important for quantifying and predicting the impact of alien species and prioritizing management based on this knowledge. Some of the parameters they suggest are conservation-related (e.g. native biodiversity, endemism and rare species, ecosystem services and ecosystem engineers). Protected areas provide opportunities for testing the results of efforts aimed at understanding the mechanisms of impacts and appropriateness of suggested management (Kumschick et al. 2015), and for quantifying these impacts (Blackburn et al. 2014; Hawkins et al. 2015). Combined with the model-species and ecosystem-integration approach advocated by Kueffer et al. (2013b), PAs could provide powerful opportunities for exploring and synthesizing processes underlying the impacts of IAPs.

Strayer (2012) argued that an improved understanding demands knowledge of the circumstances under which ecosystem change is most likely, the functions that are most often affected, and the long-term responses of ecosystems. Protected areas with relatively intact natural relationships between their components may serve this purpose well. In the same vein, PAs provide opportunities for studying whole ecosystems over large sections of landscapes, thereby providing insights into, for example, nutrient cycling and mineralization (Ehrenfeld 2003; Kueffer et al. 2013b).

Priorities for research on alien plant invasions in protected areas

The challenges associated with managing all types of threats to biodiversity are changing rapidly. The previous sections have shown that there have been substantial advances in knowledge of the occurrence of invasive plant species and their impacts in PAs. However, knowledge in this regard is fragmented and biased in several respects. In the next section we identify four broad, but not exclusive, areas that demand attention to improve our capacity to deal with the threat of plant invasions in PAs. The first deals with the need for an international group to decide on priorities, protocols, and standards; the rest are issues that will require the attention of such a group.

Establish a working group to coordinate research on plant invasions in protected areas

Global approaches are being proposed for dealing with many problems associated with biological invasions (see Packer et al. 2017). A working group with the mandate of developing a protocol for effective science-based management of alien plant invasions in PAs is urgently needed. Two examples of existing global consortia from which lessons could be learned are the global Mountain Invasion Research Network (MIREN) and Global Naturalized Alien Flora (GloNAF) programs. MIREN formed collaborative networks to examine plant invasions and management options in mountainous regions around the world (Kueffer et al. 2013a). GloNAF is an active research consortium that developed a global database on the distribution of alien vascular plant species (van Kleunen et al. 2015). For PAs, where scientific understanding is less advanced and management imperatives are required, a hybrid model that aims to both collect data and disseminate knowledge would be valuable.

Such a working group could explore questions that are of importance to PAs across species (or broad taxonomic/functional groups, such as grasses or trees) and systems at a scale beyond current capabilities, potentially in the form of multi-site model systems (sensu Kueffer et al. 2013b). Management expertise, policy development, monitoring and advances in control can be shared at the PA level where resources are often limiting and guidance urgently needed. The IUCN's SSC Invasive Species Specialist Group plays a role at an international policy level for invasive alien species to some extent, but interaction at the level of conservation practitioners is lacking. To strengthen collaboration with global PA networks, a specific task force within the IUCN World Commission on Protected Areas could be established. The level of research capacity embedded within authorities mandated to manage PAs varies greatly between regions. South African National Parks, for example, has long maintained a strong research capacity, and embedded researchers have been found to be highly connected and generally more influential across the full spectrum of research topics than external researchers (van Wilgen et al. 2016). In many other parts of the world, most research in PAs is undertaken by external researchers. Given the huge challenges, the best option to ensure adequate research effort for issues relating to invasive plants in PAs globally is improved national, regional and global networks of research expertise.

Develop standardized quantitative information on levels of invasion and protocols for monitoring

An integrated global database on the occurrence and levels of invasion of alien plants in PAs is urgently needed. This could be built and managed under the auspices of the global working group proposed above and in coordination with existing databases such as the UNEP-WCMC World Database on Protected Areas and IUCN Global Invasive Species Database. The time is ripe for such an effort—for the first time robust data are becoming available on the distribution of IAPs globally (van Kleunen et al. 2015), and an increasing number of PAs have accurate lists of species. Substantial benefits would be derived from collating accurate data specifically for large numbers of PAs worldwide. Such information is essential for: (1) better understanding of factors driving invasions in PAs at different spatial scales, and for determining whether the drivers of invasions in PAs differ from those in non-protected areas; (2) evaluating the efficiency of management within particular PAs but also at broader scales, regionally, nationally (within conservation agencies); (3) assessing changes in trends, regionally, nationally and globally, with regard to invasions in PAs. With respect to the last-mentioned point, our review has highlighted the difficulty of rigorously assessing trends in plant invasions in PAs over the past few decades; the problem is that overall the data on not only prominent and well known IAPs, but alien plant species in general are poor. One concrete suggestion towards closing this gap would be to repeat sampling of the 24 reserves worldwide that were included in the SCOPE study conducted 30 years ago (Usher 1988); such an analysis would provide an objective baseline for monitoring global trends.

Monitoring is a crucial, but often neglected, component of effective alien plant management. There is an urgent need for research to determine appropriate methods of sampling to inform monitoring programs. Protocols for standardized mapping and reporting of distribution and abundance and for effective monitoring have been developed for large areas such as South Africa's Kruger National Park (Hui et al. 2011, 2013). Similar protocols could be developed and applied globally. Metrics will need to be developed for accurate and practical mapping and monitoring of different growth forms of invasive plants, such as those developed for invasive trees (Wilson et al. 2014). In developing such protocols allowance should be made for different levels of mapping and monitoring to accommodate PAs with different levels of resources; this can be done by applying the general model recently suggested by Latombe et al. (2017) to invasions in PAs. These authors propose that the information on invasions be collected in blocks added to a minimum standard, with the amount and kind of information supplied depending on the availability of funding, starting with regularly updated lists of IAPs for all PAs. Such an approach would allow for developing countries to become the part of the global monitoring system regardless of their access to financial resources (Latombe et al. 2017).

The monitoring of invasions in PAs uses not only existing structures but also new technologies. Rapid advances are being made in the use of remote-sensing tools using aerial photography (e.g. Müllerová et al. 2005 reconstructed the course of *Heracleum mantegazzianum* invasion in a PA) and technology such as airborne imaging spectroscopy and LiDAR (Asner and Vitousek 2005; Asner et al. 2008). Freely available resources such a Google Earth are useful for mapping plant invasions in some ecosystems (Visser et al. 2014).

Science and management in PAs need to respond to different socio-political contexts

The types of PAs, their roles in national and regional conservation strategies and the options for management vary widely across the globe. Six main IUCN categories of PAs are recognized; these range, with increasing levels of protection, from protected landscapes and managed resource PAs, to national parks, to strict nature reserve protection areas and strict wilderness protection areas (see Dudley 2008 for categories). All of these areas are designated as 'protected', but the interpretation and management of the categories vary substantially, both within continents and countries and between them. This has important consequences, not only for policies relating to IAPs and approaches to managing them in different types of PAs.

It would be most informative to collect data from a network of reserves designed to cover the full range of categories of PAs across major world ecosystems and continents, in both developed and developing countries. Such data would make it possible to evaluate the role of the socio-political context in invasions of PAs and to employ appropriate management measures to respond to existing differences between nations.

As our review shows, numerous legal instruments have been in place for several decades and the number of such policies has grown recently, especially since the early 2000s. Awareness of the threats to biodiversity in PAs from IAPs is increasing. Nevertheless, an integrated international effort—involving science, management and policy, and resources to generate insights on the current status and historical dynamics of IAPs in PAs—is lacking, or at best insufficient.

Such a step is essential to pave the way for meaningful monitoring of trends, revising legislation and policies, and improving management to reduce the extent of invasions and the magnitude of impacts of invasive plants in PAs.

Acknowledgements LCF thanks South African National Parks, the DST-NRF Centre of Excellence for Invasion Biology (CIB) and Stellenbosch University, and the National Research Foundation of South Africa (Project Numbers IFR2010041400019 and IFR160215158271). DMR thanks the CIB, the National Research Foundation of South Africa (Grant 85417) and Stellenbosch University for support. PP was supported by long-term research development project no. RVO 67985939 (The Czech Academy of Sciences project no. 14-36079G, Centre of Excellence PLADIAS (Czech Science Foundation), and acknowledges the support by Praemium Academiae award from The Czech Academy of Sciences. LCF thanks PP for hosting him at the Institute of Botany, ASCR. We thank GloNAF core team members (W. Dawson, F. Essl, H. Kreft, J. Pergl, M. van Kleunen, P. Weigelt and M. Winter) for approval to use the data on the global distribution of species recorded in PAs.

Appendix 1: Search terms used to extract literature records from the SCOPUS database (12/05/2016)

((((((TITLE-ABS-KEY(invasive) OR TITLE-ABS-KEY(alien) OR TITLE-ABS-KEY(non-native) OR TITLE-ABS-KEY(weed))) AND TITLE-ABS-KEY (plant)) AND TITLE-ABS-KEY("national park") OR TITLE-ABS-KEY("nature reserve") OR TITLE-ABS-KEY("protected area") OR TITLE-ABS-KEY(wilderness)))) AND (EXCLUDE(DOCTYPE, "er")) = ***830***.

Appendix 2: Text analysis used in Figs. 4 and 5

Text analysis was carried out in R version 3.2.5 (R Core Team 2013) with RStudio version 0.99.896 (RStudio 2013) and *quanteda* (Benoit and Nulty 2016), an R package for quantitative analysis of textual data. Year of publication, title and abstracts were extracted for 830 alien plant papers in protected areas from Scopus for the period 1969–2015. Titles and abstracts were combined in a.csv file and years grouped by 20 eras. The.csv file was imported as a *corpus* {*quanteda}* object into R with publication year describing the article attributes as *docvars* {*quanteda}* and titles + abstracts representing the text to be analyzed. We created a document-feature matrix using *dfm {quanteda}*, which counts available words by article and attributes. While doing so we removed all English stopwords (very common words or adjectives that can hinder extracting keywords), numbers, punctuation marks, separators, symbols and selected words of limited value (for example, introduction, study). We also stemmed words to ensure better comparison across similar words (for example, management and manage) and removed sparse words to reduce the size of the matrix. The resulting matrix contained 2000 words across 20 eras. Using R's *corrplot* package (Wei and Simko 2016) we computed a correlation of the relative frequency of words across the different eras and conducted a Pearson's product moment correlation test at a 95% confidence level. These results were visualized using the *corrplot {corrplot}* command (Fig. 4).

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