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ALIEN FLORAS AND FAUNAS 13

Alien flora of Oman: invasion status, taxonomic composition, habitats, origin, and pathways of introduction

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Abstract We present the first inventory and status assessment of the alien flora of Oman, mainly based on field data collected from 1998 to 2021. The study provides (i) a comprehensive account of alien vascular plant species occurring in the wild in Oman, with information on their taxonomic composition. For each species information is given on (ii) invasion status (casual, naturalized or invasive), biogeography, habitat and life-form characteristics, and pathways of introduction. Further, we (iii) explain the differences in the alien species composition in different parts of the country, and (iv) analyse the drivers of plant invasions in Oman. Out of the 111 alien species reported (7.7% of the total Oman vascular flora), 34 species are casuals and 77 naturalized; of the latter seven are considered invasive. The moderate number of alien plant species is likely a result of the country's arid climate, with extremely high summer temperatures and low annual precipitation in most of its area, and the relatively long isolation of the country. The families richest in alien plant species are Fabaceae (17 species), Asteraceae (14 species) and Poaceae (12 species). More alien plants were found in northern Oman (82 species) than in southern Oman (60 species), and very few species are recorded from the central desert (7 species). The main habitats colonized

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were man-made habitats, either ruderal or agricultural. Most species alien to Oman are native to South America (49 species) or North America (43 species). This inventory provides a knowledge base for developing a national management strategy for alien vascular plants in Oman.

Keywords Exotic species · Non-native species · Tracheophytes · Invasiveness

Introduction

Environmental changes such as biological invasions are a significant aspect of the Anthropocene (Lewis and Maslin 2015; van Kleunen et al. 2015; Pyšek et al. 2017) and a major threat to biodiversity (Brondizio et al. 2019; Lowe et al. 2004). Humans have introduced thousands of species outside their native ranges (van Kleunen et al. 2018), and although most of those alien species fail to establish persistent populations in the wild, a significant part do, with numbers still increasing (Seebens et al. 2017, 2018). Globally, at least 13,939 plant species (3.9% of the extant global vascular flora) have become naturalized in regions outside of their native distribution (van Kleunen et al. 2019) and about ~2500 species are considered invasive (Pagad et al. 2015). Due to the widely documented impacts of invasive alien species on natural habitats, ecosystems, human health and economy (Pyšek et al. 2012; Kumschick et al. 2015; Nentwig et al. 2018), they have increasingly been acknowledged as a key factor of global environmental transformation (di Castri 1989; Simberloff et al. 2013; Brondizio et al. 2019; Pyšek et al. 2020). In order to manage problematic alien species, it is a prerequisite to have good inventories on their occurrences (Latombe et al. 2017; Pyšek et al. 2018).

In the 2000s, the number of detailed lists of alien plants started to increase rapidly, with e.g. the first specialized national checklists becoming available for Austria (Essl and Rabitsch 2002) and the Czech Republic (Pyšek et al. 2002). Currently, alien species inventories for various taxonomic groups are available for many countries, as well as subnational regions (starting to systematically cover the European continent by DAISIE 2009; see also, e.g., van Kleunen et al. 2015; Dawson et al. 2017; Dyer et al. 2017; Pyšek et al. 2017; Randall 2017; Pagad et al. 2018; Darrigran et al. 2020). These inventories have revealed that alien plant species have virtually invaded all parts of the world but that the numbers vary significantly among regions (van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017). A critical milestone was the compilation of the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al. 2015, 2019), which provided a worldwide overview, but also identified data gaps, particularly in tropical and temperate Asia and in many regions of Africa. Improving knowledge of the distributions of alien plant species in poorly studied regions is important for many reasons, including forming the baseline data for alien species management plans (Latombe et al. 2017) and obtaining a complete picture of global alien species richness (Pyšek et al. 2017).

Over the last four decades, intensive botanical research in Oman has taken place (for references see Patzelt 2014, 2015a), resulting in the description of more than 100 new species with restricted ranges since 1980 and documentation of many new records for the country (Patzelt 2014; Patzelt et al. 2014, 2020). While detailed studies of the vegetation and plant communities are still scarce, an overview of the main vegetation types and land units in Oman shows the varied habitats of the country (Patzelt 2015a). Here, we provide the first comprehensive inventory of alien vascular plant species of Oman and the third such study for the Arabian Peninsula (for Saudi Arabia, see Thomas et al. 2016; for Socotra see Senan et al. 2010). We provide analyses of the invasion status, taxonomic patterns, life forms and habitat characteristics, biogeography, and pathways of introduction to describe spatial and temporal patterns of the alien flora of Oman. This analysis of the patterns and drivers of species invasions in Oman contributes to reducing the existing knowledge gap on plant invasions in subtropical Asia.

Methods

Study region

The study area covers the Oman territory (Fig. 1). Oman lies between Africa and Asia, in the transition zone between the Holarctic and Palaeotropical kingdoms, as well as between subtropical and tropical

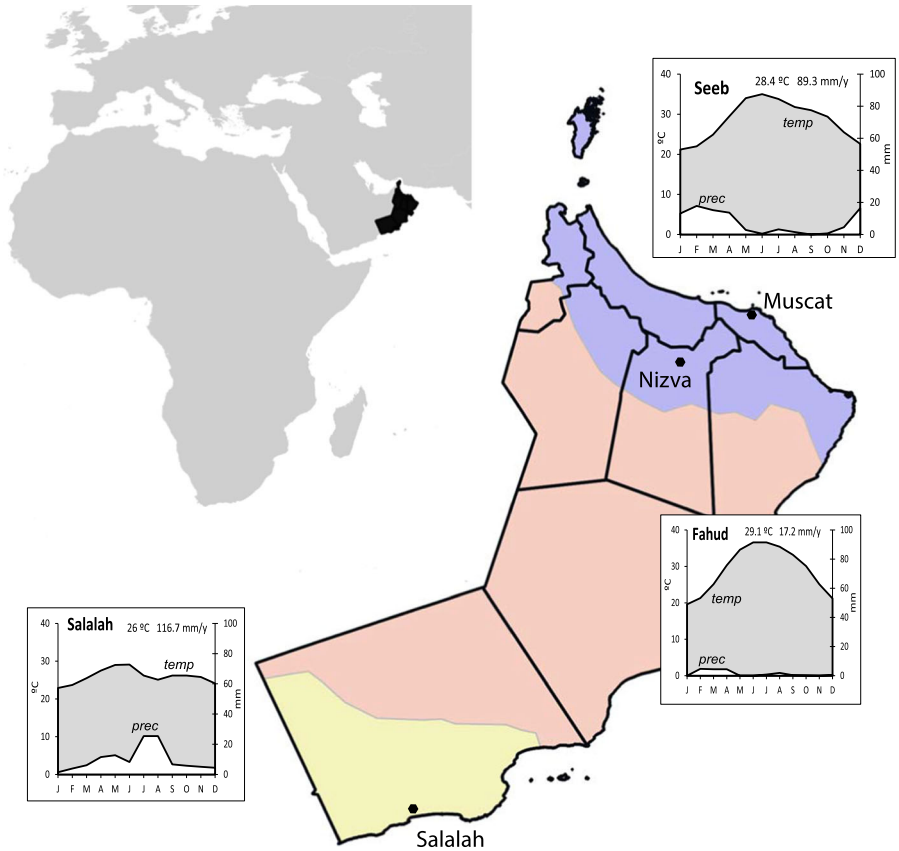

Fig. 1 Map of Oman and its main geographical features, with climagrams for northern Oman (Seeb; blue), central Oman (Fahud; orange) and southern Oman (Salalah; yellow)

climate zones, a position reflected by the presence of species from several biogeographical regions (Miller and Nyberg 1991; Kürschner 1998; Patzelt 2011, 2014, 2015a) (refer to climagrams in Fig. 1). Oman is mainly characterized by arid habitats, with most of the region occupied by sand dunes or rock and gravel desert. However, in stark contrast to the sand and gravel deserts of Oman, the country also contains a semi-deciduous cloud forest ecosystem and evergreen juniper-woodlands supporting high species diversity and many endemic species. Notable species-rich habitats include the mountain areas of southern Oman (reaching up to 2200 m), the Hajar mountains of northern Oman (reaching up to c. 3000 m), as well as the coastal areas of the central desert, all representing regional centres of plant endemism (Patzelt 2014, 2015a). The southwest monsoon vegetation of southern Oman with tropical deciduous cloud forest and tall-grass savannah is a remnant of a former moist vegetation belt of paleo-African origin, with many plant species having close links to the flora of East Africa (Kürschner et al. 2004; Patzelt 2011, 2015a).

The capital area (data from Muscat) has an average annual rainfall of 89.3 mm and the mean annual temperature is 29.1 °C (Fig. 1). In the central desert, the average annual rainfall is 17.2 mm, and the mean annual temperature is 28.4 °C. In southern Oman (Salalah), the average annual rainfall is 116.7 mm, and the mean annual temperature is 26 °C.

Definitions and delimitations

We define alien plant species as '*plant taxa in a given area whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien*' (Pyšek et al. 2004). We included an alien species if it has been documented to occur in Oman spontaneously in the wild. This

delimitation excludes plant species that are alien to Oman and are found exclusively in cultivation (for agricultural or horticultural reasons). The invasion status of alien species is described using the categories and definitions by Blackburn et al. (2011): '*Alien species that are sometimes found in the wild but do not form persistent, reproducing populations are classified as casuals (categories C0-C2), and those that form persistent populations are classified as naturalized (categories C3-E).*' If a naturalized species is reported to have an environmental and/or socioeconomic impact anywhere in the alien range, it is considered invasive (CBD 2000; IUCN 2000).

Data collection

The data were collected from 1998 to 2021 by the first author during extensive field work in all regions of the country. The research was further complemented by study of herbarium records as well as by reviewing a large body of literature. The aim was to compile a comprehensive inventory of all alien vascular plant species occurring in Oman. Herbarium vouchers collected by A. Patzelt have been deposited in the following herbaria: E (Royal Botanic Garden Edinburgh), OBG (Oman Botanic Garden Herbarium), ON (National History Museum Oman), SQUH (Sultan Qaboos University Herbarium), K (Royal Botanic Gardens Kew) and M (Botanische Staatssammlung München) (abbreviations following the index herbariorum; http://sweetgum.nybg.org/science/ih).

For each species, information on the habitat type where it occurs was recorded. The habitat classification is based on Patzelt (2015a), but for the present analysis, the habitats were assigned to broad-level types following Hejda et al. (2015) to allow for comparison with other ongoing projects on alien species. The following habitat types were distinguished and used to classify species habitat affinities: 1. Forests, 2. Open forests, 3. Scrub, 4. Grasslands (divided into 4a. natural grasslands, 4b. human-maintained grasslands. Note: habitat 4a was not considered in our analysis as it is questionable whether natural grasslands exist in Oman), 5. Sandy, 6. Rocky, 7. Dryland, 8. Saline, 9. Riparian, 10. Wetland, 11. Aquatic, 12. Man-made (divided into 12a. ruderal/urban habitats, 12b. agricultural habitats).

Based on a literature review and own observations, the plants were assigned to the following life form categories: annual herbs, perennial herbs, annual grass, perennial grass, succulents, climbers, aquatics, bulbous species, shrubs, and trees.

For each of the alien species, we compiled data on its origin, i.e., the geographic region to which it is native, from the GRIN (https://npgsweb.ars-grin.gov) and POWO (http://www.plantsoftheworldonline.org) databases. For species not covered in those database, we did internet searches (as in van Kleunen et al. 2015). Each species was assigned to one or more of the nine major biogeographically defined areas (TDWG continents) of the Taxonomic Databases Working Group (Brummit 2001). In this scheme, Central America is included in South America, and Asia is split in a temperate and tropical part. Moreover, the Pacific Islands are also considered to be one TDWG continent. Species only known from cultivation for which the native ranges are unknown were listed as 'from cultivation only', and taxa for which the geographic region is uncertain are listed as 'obscure origin'. Each species could be classified into several categories within the factors describing habitats, life forms and regions of the native range.

Statistical analysis

We tested (i) whether species habitat affinities differ among casual, naturalized and invasive species. For this, the habitat types were merged into five broad categories representing woody vegetation (habitat types no. 1–3 above), grassland (4), stressed habitats (5–8), water-related habitats (9–11) and man-made habitats (12). Further, we explored whether (ii) the alien species occurring in the north and south of Oman differ according to the pathway of introduction. We describe the patterns of differences in life history and origin among the casual, naturalized and invasive species, but we could not statistically test the patterns due to a high number of zeros in individual categories. All tests were done in R (ver. 3.6.2) by using species counts analyzed by generalized linear models with a log-link function and Poisson distribution with control for overdispersion (if needed using the quasi-Poisson setting). To test in which category the counts were lower or higher than expected by chance, adjusted standardized residuals of G-tests were compared with critical values of a normal distribution (Řehák and Řeháková 1986). All tests and comparisons were made

on the pool of naturalized species if not mentioned otherwise.

Results

Alien flora by invasion status

A total of 111 alien vascular plant species are recorded from Oman; a complete list of species with information on their taxonomy, life form, origin, invasion status and habitats is provided in Supplementary Table 1. Thirty-four species are casuals (31%) and 77 are naturalized (69%), of which seven are considered invasive. The overall contribution of naturalized alien species to the total flora of the country is 5.3%; casual species represent 2.4%. Table 1 lists the top 10 alien species based on the number of habitats in which they have been recorded.

Taxonomic composition

The 111 alien species represent 38 families. The families richest in species are Fabaceae (17 species), Asteraceae (14 species), Poaceae (12 species), Solanaceae and Amaranthaceae (6 species each), and Convolvulaceae (5 species) (Supplementary Table 1). Eighteen families (49%) were represented by a single species. Amongst the 77 naturalized plant species, four plant families, Fabaceae (12 species), Asteraceae (9 species), Poaceae (7 species) and Solanaceae (6 species) constituted almost half of the species (45%). The genera richest in alien species are *Ipomoea* (4 species), *Amaranthus, Cenchrus*, *Euphorbia* and *Senna* (3 species each), while 10 genera are represented by two species and 17 genera by one species (Supplementary Table 1).

Life forms

The majority of naturalized alien plants in Oman are annual herbs, constituting 32% (36 species) of all aliens, followed by perennials making up 23% (25 species) (Fig. 2). Shrubs constituted 10% of all alien species, climbers 9.1%, trees 6.4%, annual grasses 5.5%, perennial grasses and succulents each 4.6%, and aquatics 2.8%; bulbous plants were neglectable (one species only). The seven invasive species were representatives of four life forms: three annual herbs, one perennial herb, two trees, and one shrub.

Habitats

The naturalized alien species in Oman are mainly reported from two types of frequently disturbed habitats – 63 species (of which 40 are naturalized, including invasives) occur in agricultural habitat and 53 (44 naturalized) in ruderal habitats. These two habitats harbour 84% of all recorded naturalized alien species. Eighteen species (14 naturalized) were found in wetlands (including moist and wet areas in wadis with permanent water bodies in part of their course as well as periodically flooded areas in wadis), 16 (15) in anthropogenic grasslands, 15 (14) in open forests, and 12 (12) in scrubland (Fig. 3A). Among habitats harbouring more than 12 aliens, the proportion of invasive species was highest in scrubland, saline and riparian habitats (50%), followed by open forest (40%) (Fig. 3B).

Table 1 The 10 most represented alien plant species in Oman, based on the number of habitats in which they have been recorded

Species	Family	Life form	Habitats	Status
Prosopis juliflora (Sw.) DC	Fabaceae	Tree	11	Invasive
Alternanthera pungens Kunth	Amaranthaceae	Annual herb	7	Invasive
Parthenium hysterophorus L	Asteraceae	Annual herb	6	Invasive
Leucaena leucocephala (Lam.) de Wit	Fabaceae	Tree	5	Invasive
Nicandra physalodes (L.) Gaertn	Solanaceae	Annual herb	5	Invasive
Impatiens balsamina L	Balsaminaceae	Annual herb	4	Invasive
Lantana camara L	Verbenaceae	Shrub	4	Invasive
Cucumis sativus L	Cucurbitaceae	Climber	4	Naturalized
Argemone mexicana L	Papaveraceae	Annual herb	4	Naturalized
Portulaca oleracea L	Portulacaceae	Annual herb	4	Naturalized

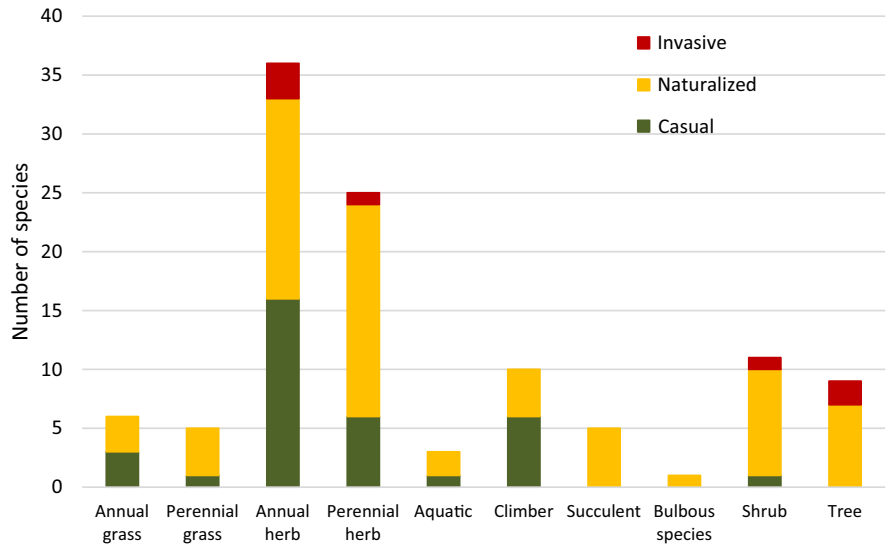

Fig. 2 Life forms of alien species in Oman

Casual species occurred in seven out of the 13 habitats, naturalized (but not invasive) in nine, and invasive in 11 habitats. The greatest number of casuals (23 species; 68%) was found in agricultural habitats, followed by ruderal habitats (9 species). Casuals were found in only five natural habitats. Forty-two of the 70 naturalized species (excluding the invasive ones) were not found in natural or semi-natural ecosystems at all, i.e., they were only recorded from disturbed and modified ecosystems: agricultural and ruderal (habitats 12a and 12b). Sixteen naturalized species were predominantly found in modified ecosystems but occurred additionally also in one natural habitat. One species each was found in dryland habitats on sandy or rocky substrate, and two species each were found in saline habitats.

The distribution of alien species in the broad habitat groups significantly differed by status, but only for invasive species ($F_8 = 3.58$, $p < 0.001$). There were more invasive species than expected by chance in stressed habitats and fewer in man-made habitats (Fig. 3B). The seven invasive species have the broadest habitat niches, with *Prosopis juliflora* occurring in 11 of the 13 habitats, *Alternanthera pungens* in seven habitats, *Parthenium hysterophorus* in six, and *Leucaena leucocephala* and *Nicandra physalodes* in five habitats.

Most alien plant species were recorded from northern Oman (82 species; 74%), while 60 species (54%) were recorded from southern Oman and only six species (6%) from the central desert (Fig. 4).

Origin

The majority of the alien plants in Oman originate from South America (55 species; 44%; Supplementary Table 1; Fig. 5), followed by North America (31 species; 28%), temperate Asia (30 species; 27%), tropical Asia (28 species; 25%), and Africa (20 species; 18%). A limited number of species originate from Europe (11 species; 10%) and Australasia (5 species; 5%).

Eight species are of obscure origin and three species are known as cultivated forms only. The dominance of the Americas as a source region is even more pronounced for the subset of invasive species, with these two continents accounting for all but one species (i.e., 86% of the invasive species). The only invasive species not originating from the Americas is *Impatiens balsamina*, coming from tropical Asia.

Pathways of introduction

Forty-six species (37 naturalized) have been brought to Oman unintentionally (42%), 43 (22 naturalized) species (39%) have been imported for agricultural use, and 27 (23 naturalized) species (23%) are associated with horticulture and used as ornamental plants along roadsides, and in parks and gardens. All species

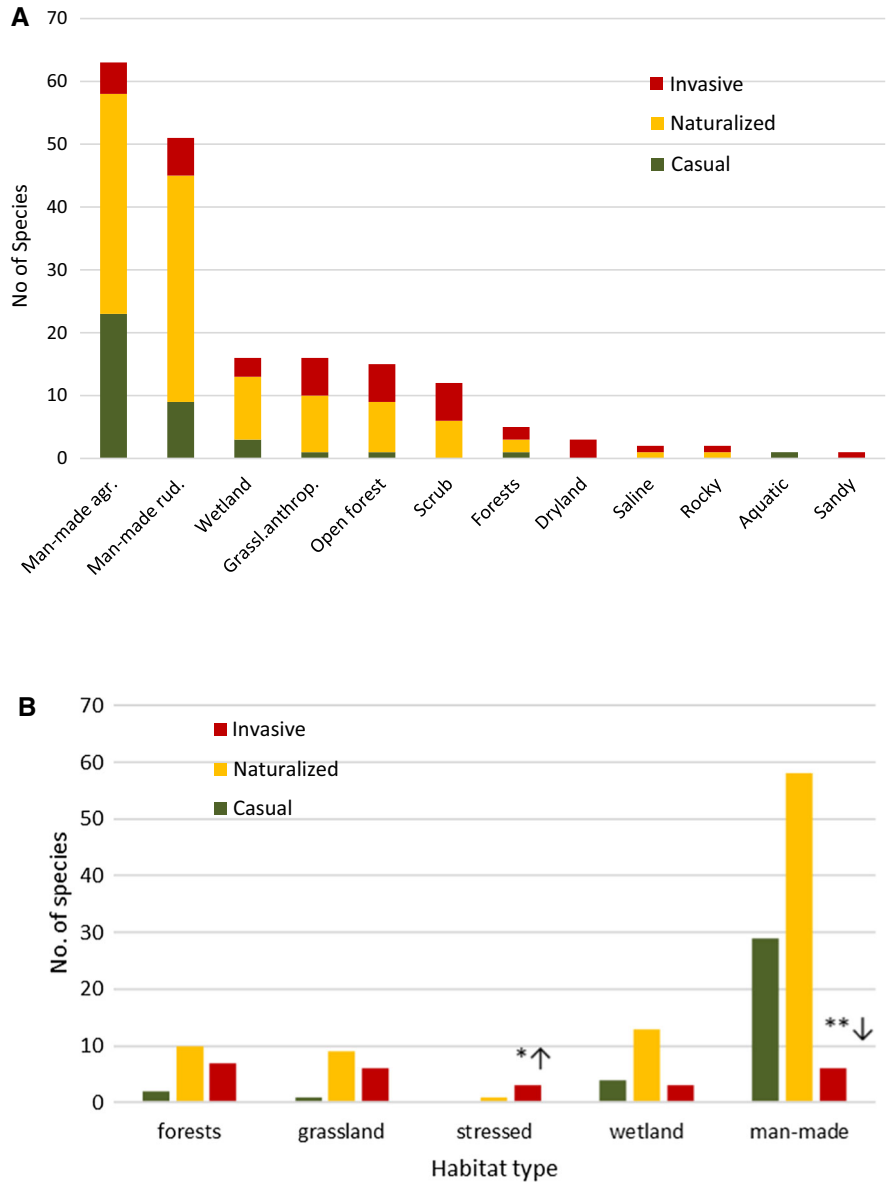

Fig. 3 Numbers of naturalized species assigned to individual habitats (**A**) and to broad habitat categories (**B**). Arrows indicate whether the observed counts are above or below the counts expected by chance. * < 0.05, ** < 0.01 Stressed habitats refer to dryland, saline and rocky

brought in intentionally have escaped from their intended use in agriculture or horticulture. The pathways of introduction to northern and southern Oman significantly differed ($F_2 = 3.36$, $p = 0.03$), reflecting that unintentional introductions are under-represented in northern Oman and over-represented in southern Oman compared to the numbers expected by chance.

As part of this study, *Sclerocarya birrea* (A. Rich.) Hochst. was newly recorded from several villages in northern Oman, always growing close to irrigation channels. The mature plants may have been planted as seeds, but also young plants were observed in the understory of old trees. As it seems highly likely that the young trees have seeded naturally, we treat the species here as naturalized.

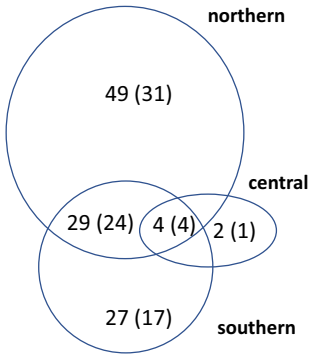

Fig. 4 Size-proportional Venn diagram on the distribution of alien (total number of casual and naturalized; in brackets only naturalized) species in the Oman regions, with the cross-sections indicating the numbers of species shared between regions

Discussion

Structure and composition of the alien flora: invasion status, taxonomy, and life forms

This inventory of the alien plants of Oman is primarily based on extensive fieldwork from September 1998 up to March 2021, supported by literature analysis. Thus, it reflects the up-to-date state of plant invasions in Oman. We found that the alien flora consists of 111 alien species, which represent 7.7% of the total flora of the country. The flora of Oman was reported to include 1407 species (Patzelt 2015a). However, is is expected that numbers will be further increasing because of the discoveries of new native species, as well as new records of alien species. Compared to many other regions around the world, the number of alien plant species in Oman is at a low level (Pyšek et al. 2017; Essl et al. 2019). This is to a large degree due to the extremely arid climate lasting for several months a year, but probably also a result of the international isolation of the country until the 1970s.

A comparison with the global naturalized alien flora (Pyšek et al. 2017) and invasive flora (Willis 2017) reveals that the three globally most represented families (Asteraceae, Fabaceae and Poaceae), in terms of species richness, are also richest in alien species in Oman. The predominance of those families among alien species is not surprising given that they are among the largest families globally. However, the Fabaceae and Poaceae have globally still more naturalized species than one would expect based on the total number of species in those families, and many of the most widespread alien species are Asteraceae (Pyšek et al. 2017). Of the 11 most widely distributed naturalized alien species worldwide (Pyšek et al. 2017), three also occur as aliens in Oman, and six others are considered native in Oman. Three out of the global top five of the most widely distributed invasive species (*Lantana camara, Pontederia crassipes* and *Leucaena leucocephala*) also occur in Oman as alien species, and two of them are invasive (*L. camara* and *L. leucocephala*).

In the alien flora of Oman, annual and perennial herbs largely prevail (56%), with relatively few shrubs and trees present (17%). This corresponds well with

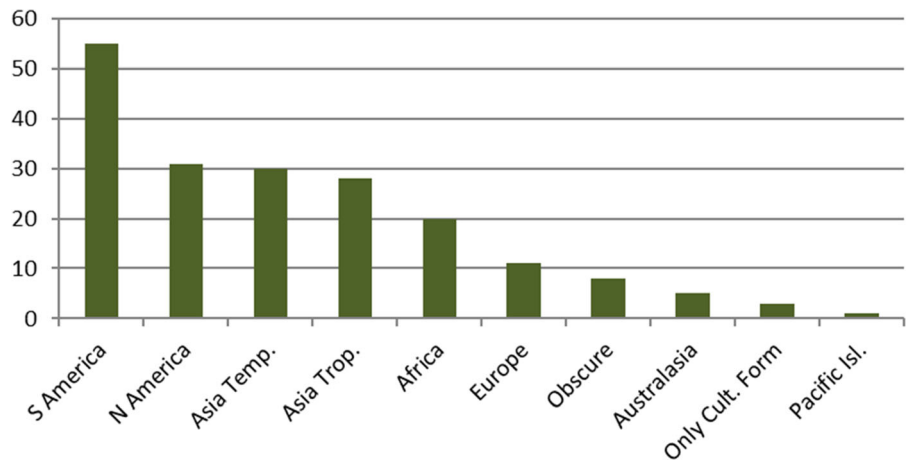

Fig. 5 Origin of the alien flora of Oman shown by region (TDWG continents). The proportional representation of aliens with particular origins within each region exceeds 100% as some species' native distribution ranges cover more than one region. Species with unclear origin are shown in the category 'obscure'

the native flora, where annual and perennial herbs constitute 62% of the species, whereas shrubs and trees constitute 15%. Almost 50% of the global flora is woody (FitzJohn et al. 2014), and 32% of all aliens are woody (Pyšek et al. 2017, p. 235–237), but woody species are strongly under-represented as aliens as well as native species in Oman. This pattern is likely due to the harsh arid climatic conditions in most of Oman, which are unfavourable for the establishment and growth of woody species. Herbs have short generation times and are therefore likely to establish and spread rapidly and use the short cool and moist times of the year for reproduction. Especially annual species may complete their short life cycle in just a few weeks and are therefore well adapted to arid climates (Mulroy and Rundel, 1977).

Among the seven invasive species in Oman, four are herbs that form large populations and dominate natural plant communities (*Impatiens balsamina*, *Nicandra physalodes* and *Parthenium hysterophorus*) or displace native species (*Alternanthera pungens*). The other three invasive species are woody (*Lantana camara*, *Leucaena leucocephala* and *Prosopis juliflora*) and have allelopathic effects on native species. In case of *P. juliflora* (e.g., Warrag 1994), there are reports of complete dominance of natural habitats in Oman (Patzelt and Lupton 2021).

Temporal patterns and pathways of introduction

In European countries, alien floras can be distinguished into two groups based on their residence time – archaeophytes and neophytes. However, this classification is rarely used in other regions of the world and has not been applied to the present dataset, as no written sources are available regarding Oman's flora before the middle of the nineteenth century. This makes it impossible to infer whether a given species had been introduced before or after 1492.

The first records of vascular plants of Oman date back to March and April 1838, when Pierre Aucher-Éloy made a comprehensive collection of plants from northern Oman (then called the Immamat of Muscat). His collection included 218 species, out of which 34 were new to science. The following seven species, listed in our alien vascular plant species inventory, were already noted and collected by Aucher-Éloy: *Momordica balsamina, Ocimum* sp., *Senna sophera, Oxalis corniculata*, *Ruta chalepensis, Datura metel* (today identified as *D. innoxia*), and *Eleusine coracana*.

For southern Oman (Dhofar), the first list of species was only published in 1988 (Miller and Morris, 1988), listing 736 species. In their list, 26 alien species were recorded, which are included in the present inventory. We here list 59 alien vascular plant species for southern Oman, 33 species more than in the inventory of 1988. Interestingly, four of the seven invasive species (*Prosopis juliflora, Leucaena leucocephala, Parthenium hysterophorus* and *Lantana camara*) were not listed 33 years ago. As it is highly unlikely that they were overlooked by the earlier study, it must be assumed that they were not present then. For some invasive species, the date of the first observation in Oman has been recorded, e.g., *Parthenium hysterophorus* (Patzelt and Lupton 2021).

Many alien plant species have been imported intentionally into Oman, mostly for ornamental planting and agriculture. As it can be assumed that most if not all species for ornamental horticulture were only introduced to Oman from the late 1970s onwards, the pressure through propagules of these species has dramatically increased in the last four decades. Many horticultural species have been introduced even more recently, and the import of new species for horticulture is still ongoing. It is likely that in the future, further species might escape amenity horticulture and become either casual or naturalized species.

For the plants that escaped from traditional crop cultivation, it can be assumed that most have been brought to the country hundreds if not thousands of years ago, as the oldest oases in northern Oman are up to 5000 years old (Nagieb et al. 2004), and crops have been cultivated since then in irrigated oasis settlements (Gebauer et al. 2007; Hammer et al. 2008; Patzelt 2010). It is hypothesized that agricultural weeds found in the traditional oasis systems constitute species that are likely to have been introduced unintentionally, with their seeds and diaspores contained in the soil of the introduced cultivated crops (e.g., with pomegranate, apricot, and peach from the Eastern Mediterranean region) or as crop contamination. These plants spread with agriculture thousands of years ago and have over the course of time occupied moist ecological niches in Oman, mainly in cultivated fields and ruderal places in oasis settlements.

A number of species introduced as agricultural crops or for amenity horticulture has not yet been

recorded outside of cultivation (e.g., *Acacia farnesiana, Antigonon leptopus, Casuarina equisetifolia, Gomphrena globosa, Momordica charantia, Psidium guajava*), although they are considered to have potential to escape from cultivation in the future (i.e., to become alien species).

Climatic and ecological constrains to invasions by alien plants

The trend noted by Pyšek et al. (2017) that the accumulation of alien species is rather fast in colder and Mediterranean regions and slow in arid zonobiomes is supported by the present analysis. The Arabian Peninsula with its arid climate is characterized by low regional invasibility, and Oman has been identified as a coldspot region for alien species richness (Dawson et al. 2017). While it is assumed that climate change will increase the naturalization risk from alien garden plants in Europe (Dullinger et al. 2017; Mayer et al. 2017), the same will not hold true for the Arabian Peninsula. Temperatures in Oman have increased significantly over the past decades; minimum temperatures rose by 3–6 °C from 1980 to 2008, while precipitation has decreased (AlSarmi and Washington 2011). The anticipated climate change will thus further reduce the invasibility of Oman and the Arabian Peninsula. Moreover, alien species can make the aridification even worse as alien invasive species have been reported to consume more water than native flora (Le Maitre et al. 2000; Zavaleta 2000).

Many habitats in Oman are characterized by a variety of environmental stress factors such as low nitrogen and phosphorus content, saline or alkaline soils, serpentine soils, low soil moisture, shallow and rocky soils, low precipitation, and high temperatures (Zaffermann et al. 2015). The invasion of habitats under such harsh conditions is likely to be additionally limited by the relatively low arrival rates of propagules compared to ecologically less extreme habitats. Yet, we found that invasive species are over-represented in stressful habitats, compared to naturalized and that are completely missing from such conditions.

Globally, most naturalized plants have been introduced for economic uses (van Kleunen et al., 2020). Similarly, we found that most aliens in Oman were introduced for agricultural or horticultural purposes. However, such species are less likely to be introduced to harsh habitats that are unsuitable for agriculture and gardening. Both propagule limitation and invasion resistance may thus simultaneously contribute to the low numbers of alien plants in many habitats in Oman and the Arabian Peninsula, as it has been shown for other harsh environments (Zaffermann et al. 2015).

Spatial patterns: local variation in the level of invasion

The geographic distribution of alien plant richness in Oman can be explained by several factors. The most important are climate and habitat availability. It is not surprising that the number of alien species is much lower in the central desert, given the extreme arid climate, low soil availability (mostly gravel and rock) and low fertility (Patzelt, 2015a, b). Indeed, precipitation is one of the key climatic factors shaping the richness of alien floras (Lambdon et al. 2008). In contrast, the oasis ecosystems in northern Oman and the monsoon-affected vegetation in southern Oman provide less stressful habitats for plants and have higher alien species richness.

Although southern Oman locally offers favourable climatic conditions for the invasion of alien vascular plant species, fewer were recorded from there than from northern Oman (59 and 79, respectively). This is surprising, as the south is affected by the southwest monsoon and provides relatively moist climatic conditions for 3–6 months per year. The lower number of alien species is probably a result of three factors. Firstly, until recent years, there was limited ornamental horticulture in southern Oman, mainly restricted to the city of Salalah. Secondly, agricultural areas in southern Oman, except for the Salalah city, are also limited, as local people are traditionally herders and therefore, there is no history of maintaining (permanent) agricultural areas. Thirdly, large areas of southern Oman were very thinly populated until two decades ago. Human population density is frequently a key factor positively correlated with naturalized species richness, as it has been shown for Europe (Pyšek et al. 2010b). The increase in human population size in southern Oman in the last two decades may not yet have resulted in increased alien species richness due to invasion time lags (Crooks 2005), resulting in an invasion debt (Essl et al. 2011). It is thus postulated that the number of alien species in southern Oman may increase in the near future.

The low number of species recorded from the central desert is a result of extreme environmental conditions, but also suggests that this remote region might still be underexplored in terms of its alien flora. It is assumed that at least the following species are present but not yet recorded as alien species: *Catharanthus roseus, Albizia lebbeck, Azadirachta indica, Bougainvillea* cf. *spectabilis, Oxalis corniculata, Cenchrus purpureus* and *Solanum lycopersicum*. In particular the surrounding area of oil-field accommodation should be systematically surveyed, as alien plants are introduced intentionally to these accommodation villages for ornamental and agricultural purposes. The much higher number of alien plants in northern Oman is likely a result of the man-made habitats present, such as oasis settlements, as well as the much higher human population. Human disturbances promote invasions (Davis et al., 2000; Lockwood et al., 2007), and indeed several observational and experimental studies provide evidence for this (Colautti et al. 2006; Kempel et al. 2013).

Human population is directly related to introduction pressure (Pyšek et al. 2010b; Dawson et al. 2017). Disturbance of soil and vegetation is a prerequisite and assisting feature for the establishment of many species, and such disturbance can be expected to increase with human population density (Chytrý et al. 2008a). This may explain why the number of alien species in Oman is highest in ruderal and agricultural ecosystems, as these are the most disturbed and most densely populated habitats, confirming the patterns reported from other parts of the world (e.g., Chytrý 2008b, Pyšek et al. 2010a, 2010c). It has been speculated that disturbances fail to support naturalization if they exceed a certain threshold (Pyšek et al. 2017). Agriculture in the traditional oasis settlements in northern Oman is still mainly for subsistence. No pesticides or herbicides are used for the control of weeds, and crops are still mainly fertilized with animal manure, minerals and ashes (Bürkert and Schlecht 2010; Patzelt 2015b). Thus, the disturbances are at low to intermediate levels that support the invasion of alien species. Several alien plants have in recent years been newly reported from the oasis ecosystems (Patzelt et al. 2014, 2020), showing that invasion of alien species is an ongoing process in Oman.

Origin of the Oman alien flora: different from global patterns

With regards to the biogeographical classification, the native ranges of the naturalized flora of Oman include the tropical and subtropical regions of the world. For most of the species, however, the native ranges reach into temperate regions, and the available distribution data do not allow to classify clearly the (sub-)tropical origin. The description of ranges is relatively rough, referring to the TDWG continents (Brummit 2001). Globally, the continents that contribute most to the naturalized alien flora are temperate Asia (20.3%), North America (17.1%) and Europe (15.1%), followed by Africa (14.3%) and South America (12.8%) (Pyšek et al. 2017). This is in sharp contrast to Oman's naturalized flora where the prevailing donor regions are South America (50%), temperate Asia (27%), tropical Asia (25%), and North America (18%). Particularly, the low number of species from Europe is remarkable given that Europe, together with Asia, were the main economic partners for Oman for centuries. Possibly, there are only a few European species that are adapted to the arid climate of Oman. Similarly, it was recently shown that only few European species have invaded Sudan, most likely due to unsuitability of the climate there (Omer et al. 2021). It is also surprising that there is only a limited number of alien species from Africa (20 species; 18%). Perhaps because tropical African species constitute a major part of the native flora of southern Oman (Patzelt 2014; 2015a), the African species that find suitable habitats in Oman are already present. The preponderance of species from the Americas, in particular South America, may indicate that most alien species have only been introduced in recent decades when trade exchange with the Americas became more frequent.

Comparison with other countries in the region

Apart from this publication, only two other compilation of alien species exist for the Arabian Peninsula (Senan et al. 2010; Thomas et al. 2016). The flora of Saudi Arabia (2,400,000 km^2) is estimated to have $\sim$ 2100 species (Miller & Cope, 1996), which is about one-third richer than Oman with its $\sim$ 1443 species (A. Patzelt, unpublished data), but the alien plant list for Saudi Arabia includes only 48 species (Thomas

et al. 2016). From Socotra, 87 alien taxa represent approximately 9% of the total flora (Senan et al. 2010). Most were introduced in the past 10 to 20 years. Oman with 111 alien species is thus the country with the highest reported alien plant richness in the Arabian Peninsula. This is surprising given that Saudi Arabia is almost seven times larger than Oman and that the numbers of naturalized species are typically closely correlated with those of native species (Pyšek et al. 2017). The relatively low number of alien species reported for Saudi Arabia, therefore, suggests that this country might still be underexplored in terms of its alien flora.

Impact

Due to the extreme aridity of most areas in Oman, the number of species currently considered to be invasive as well as that of species with a risk of becoming invasive in the future is comparatively small. The only plant species with a massive impact on native species is *Prosopis juliflora*, whereas the other invasive species have only local to moderate impacts (Patzelt and Lupton, 2021). For most invasive species, holistic national management programs could either eradicate the species from Oman or ensure that the species of concern does not spread further. It is highly recommended that for species which still have localized distributions (e.g., *Lantana camara*, *Sesuvium portulacastrum*) an immediate eradication program be started.

Conclusions and outlook

This publication presents the first inventory of alien vascular plants for Oman, using standard criteria. The compilation of such an inventory is essential for research and as baseline data for guiding conservation policies as well as to prevent or mitigate the impacts caused by alien species on biodiversity and human livelihoods. In terms of knowledge of the alien flora of Oman, our study can trigger additional research within the country, as for many naturalized species, in particular those that are invasive, precise information on their distributions and population sizes is still lacking. Gathering further information on absolute numbers and population sizes and, if possible, monitoring the dynamics of alien species over time will form a solid basis for any planning with a temporal perspective.

The data presented here are essential for informing future policies and the development of an alien species management strategy and its implementation. Oman does not yet have an invasive species management plan. It is hoped that this publication enables the decision-makers to take appropriate action to prevent the further spread of alien plant species, set up a monitoring and impact-assessment program and control the invasive species.

Data availability statements

The data supporting the results reported in the article can be found in Supplementary Table 1.

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Authors' contributions AP was the project leader, compiled all field data and the inventory, and wrote the first version of the article. PP and MvK were involved in conceiving the idea, implementing paper structure and writing the paper. JP conducted the statistical analyses.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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