The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea

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Abstract   Invasion by exotic species is recognized as one of the major threats to biodiversity. The effects of invasion by *Opuntia ficus-indica* (Cactaceae) on the species diversity, richness and composition of invaded communities were studied at three sites in the highlands of Eritrea, East Africa. This paper investigates whether the presence of *O. ficus-indica* causes a negative effect on the native biodiversity in a region rarely studied so far. The vegetation in invaded and uninvaded plots with similar habitat conditions was sampled and differences in the species composition, diversity and richness were compared between the plots. The overall plant species composition differed significantly with invasion by *O. ficus-indica*. The invasion by *O. ficus-indica* also led to a significant homogenization of community compositions. The species richness and Shannon diversity index did not differ significantly between the invaded and uninvaded plots. Nevertheless, we still detected species with significantly lower occurrence in the invaded plots (*Psiadia punctulata*), but also species which preferred invaded plots (*Plectranthus hadiensis*). We conclude that *O. ficus-indica* exerts a negligible effect on the species diversity and richness but that it affects species composition and that there are species which suffer due to its presence. Due to the continuous pressure of the invasion by *O. ficus-indica* on the species composition and dry climates, further homogenization in the native species diversity is to be expected in the future for the highlands of Eritrea.

Keywords   Eritrea · *Opuntia ficus-indica* · Plant invasions · Species composition · Species diversity · East-African highlands

Introduction

Invasion by introduced exotic species is recognized as one of the major environmental problems and threats to biodiversity (Di Castri et al. 1989; Di Castri and Hansen 1990; Williamson 1996). Many of the deliberate introductions relate to the human interest in nurturing species for agricultural, forestry or ornamental uses (Staples 2001). Invasion by exotic plant species can significantly alter the native plant community composition and ecosystem processes (Vilà et al. 2011), although the types and magnitudes of...
impacts of individual invasive species can vary with the type of ecosystem or invasive species (Fridley et al. 2007; Stohlgren and Rejmánek 2014). Even though some studies argue that plant invasions rarely cause biodiversity loss (Sax et al. 2002; Gurevitch and Padilla 2004; Maskell et al. 2006; Stohlgren et al. 2008), others have shown significant declines in biodiversity due to introduced invasive plants (Wicke et al. 1998; Pimentel et al. 2001; Pauchard and Shea 2006). Various invasive plants are also known to change species composition or diversity (Vila et al. 2006; Gaertner et al. 2009; Hejda et al. 2009; Powell et al. 2011), decrease ecosystem productivity and alter the rate of nutrient cycling (Liao et al. 2008; Ehrenfeld 2003), and hence impact ecosystem services and human well-being (Pejchar and Mooney 2009). Moreover, invasive species have been considered important agents in homogenizing plant communities at spatially different levels (Dar and Reshi 2015; Lososová et al. 2016; Price et al. 2018). Biotic homogenization is the process of increasing similarity among previously distinct communities within a specific region (Olden and Rooney 2006; Smart et al. 2006) and plant invasions may cause homogenization of the natural habitats by adapting to the new environmental conditions and dominating the native vegetation (Van Kleunen et al. 2010; Sol et al. 2012; Morri et al. 2019).

Invasiveness is influenced by species traits and describes the extent to which an alien species can overcome biotic and abiotic barriers to establishment and spread in a new environment (Richardson and Pyšek 2006; Wilson et al. 2007). Invasive plants are successful due to several reasons. They can produce many viable seeds, be unpalatable to herbivores, easily establish in different environments, tolerate highly stressful conditions and/or have an ability to readily regenerate from seeds, stems or roots. These features enable them to survive, spread and ultimately impact the native ecosystem (Obiri 2011). *Opuntia ficus-indica* (prickly pear), native to Mexico, is an exceptionally successful drought-tolerant invasive cactus that grows in arid and semi-arid areas. *Opuntia ficus-indica* is considered as an ecosystem engineer as it modifies the habitats of the indigenous plant species and dependent animals (Jones et al. 1994). This species impedes the movement of livestock and humans as it forms impenetrable thickets. It displaces native plants and reduces the carrying capacity of pasture and particularly threatens large-scale cattle ranching (Obiri 2011). *Opuntia ficus-indica* occurs in countries where it has been cultivated and is invasive in Australia, Eritrea, Ethiopia, South Africa, Hawaii, USA and also to some extent in Somalia and Yemen (Brutsch and Zimmermann 1995), as well as in the tropical forests and rangelands of Kenya and Tanzania (Obiri 2011, Oduor et al. 2018). Additionally, Novoa et al. (2015) report that *O. ficus-indica* is the most widespread invasive cactus distributed outside the native range in 22 different countries.

In Eritrea, *O. ficus-indica* is highly invasive and abundant with an estimated cover of about 10,000 ha in the highlands, especially on the eastern escarpments (Bein et al. 1996). There is no clear evidence as to when *O. ficus-indica* was introduced into Eritrea, but it is assumed to have been planted in the southern parts of the highlands as early as 1839 and was then brought to the central highlands (NEMP-E 1995). The fruit of *O. ficus-indica* is popular as food for humans as well as animals. Outweighing its benefits, *O. ficus-indica* is invading the highlands, potentially causing changes in the ecological functioning of the native Afromontane forests, which, according to White (1983), is one of the major regional centres of endemism. The Invasive Woody Plant Database comprises over 5000 publications on species invasiveness, whereby only 6% refer to tropical Africa (Obiri 2011). This implies that the pressure on the native diversity in the region has rarely been studied and we are unaware of any comparable studies in Eritrea.

This paper analyses the ecological impacts of *O. ficus-indica* on the native plant diversity in Eritrea. We hypothesized that the spread of *O. ficus-indica* affects the composition, diversity and richness of the native plant species. Additionally, we measured environmental factors that potentially influence the invasion of the plant. We hypothesized that *O. ficus-indica* thrives in higher elevations, steep slopes and shallow soil depths. This was mainly because *O. ficus-indica* has been planted in Eritrea for soil conservation and to prevent erosion on steep slopes and higher altitudes (Bein et al. 1996). All these assumptions were tested using original field data, based on the comparisons of vegetation with and without *O. ficus-indica*.
Materials and methods

Study species

*Opuntia ficus-indica* is an evergreen perennial plant that can grow up to 5 m in height. The species has succulent stems that are formed as a sequence of flattened segments, the cladodes, which generally have an elliptical base that supports the greatly enlarged, flattened upper portion. *Opuntia ficus-indica* has spines, morphologically corresponding to leaves. Its flowers (5–10 cm in diameter) are sessile and solitary, and the fruits are berries that are 4–8 cm in diameter (Gimeno and Vilà 2002) with an average of 273 seeds per fruit (Barbera et al. 1991). Nieddu and Chessa (1997) found the germination of the *O. ficus-indica* seeds reaching up to 90% in growth chambers with a day/night temperature of 30/20 °C, but only reaching 55% when seeds were kept at room temperature and 43% when seeds were placed outdoors. The seeds are usually dispersed after consumption by humans, birds and other animals (endozoochory). Furthermore, vegetative propagation occurs through cladodes readily taking root upon falling to the ground and conspicuous patch formation is an important factor in the persistence of local populations of the plant, although seedling recruitment is essential for expanding the geographic range and establishment in new areas (Gimeno and Vilà 2002).

Study site

The study was conducted in the central highlands of Eritrea, where *O. ficus-indica* grows vigorously and is abundant. The central highlands lie at an altitude over 1500 m with a mean annual rainfall of 500 mm. It is an area with a warm to cool semi-arid climate and potential evapotranspiration ranging between 1300 and 1800 mm. In this area, the rainy season normally lasts about three months, beginning in June and ending in August. Besides heavy rain, occasional showers come in March and April (Ogbazghi and Stillhardt 2011). The vegetation map of Africa by White (1983) lists 20 major regional centres of endemism, of which four (the Sudanian, Somali-Massai, Afromontane, and Sahel regions) are well represented in Eritrea. The natural vegetation of the study site is the dry part of the Afromontane regional centre of endemism. The flora as a whole is estimated to contain over 4000 taxa, of which 75% are likely to be endemic to the Afromontane regional centre (Ogbazghi and Stillhardt 2011). Despite this regional taxonomic richness, plot-level species richness is remarkably low, especially compared to the richness of higher taxonomic units (Hamilton 1976; Bekele 1994; Tura et al. 2017).

Sampling design

The ecological data were collected from June to August 2018. The fieldwork was conducted during and shortly after the rainy season for an effective sampling of the existing plant species because most of them sprout, leaf out and/or produce fruits during this time. Representative original habitats were selected at three different sites (Fig. 1) to identify and assess the ecological impacts of *O. ficus-indica*. The aim was selecting a wide range of habitats where *O. ficus-indica* has established sustained populations in the central highlands of Eritrea: (a) a relatively humid site in which *O. ficus-indica* was historically favoured by people for collection of fruits and free grazing takes place (site 1), (b) a rocky site and relatively dryer than the other two sites (site 2), and (c) a site protected from human use (site 3). This selection of contrasting sites provided a general picture of invasive success and its impact in the Eritrean highlands. At each site, we compared *O. ficus-indica* invaded areas with surrounding uninvaded areas, in which the uninvaded control plots were located as close to the invaded plots as possible to have similar site conditions (5–10 m distance). A total of 36 pairs of plots (12 pairs for each site and each plot measuring 10 × 10 m) were sampled to assess the potential effects of *O. ficus-indica* (Table 1). The pairs of plots represented the *O. ficus-indica* invaded group and the non-invaded or control group. In each of the plots, the floristic composition of the understory vegetation, the shrub layer and the tree layer were recorded and their covers estimated. The sampling approach was to examine species composition and to compare species richness and diversity estimates between *O. ficus-indica* invaded and uninvaded plots. Plant species were identified following Hedberg and Edwards (1989); Edwards et al. (1995); Edwards et al. (1997); Edwards et al. (2000); Hedberg et al. (2003); Hedberg et al. (2006); Mesfin (2004) and Bein et al. (1996).
accurate identification of some species, specimens were taken to the Herbarium of the Eritrea Institute of Technology. Additionally, environmental factors such as elevation in meters above sea level, soil pH measured in water, slope in degrees and soil depth in centimetres were measured. An average value of samples from three sides of each plot was taken to equally represent the environmental parameters.

Statistical analyses

We calculated differences in the composition of vascular plant species between the invaded and unininvaded plots of the three sites using an analysis of similarity (ANOSIM) with the function anosim in the vegan package (version 2.5-6; Oksanen et al. 2019). To assess the degree of similarity in community composition between plots, we computed the Bray–Curtis dissimilarity index. This was performed based on the native species abundance. The values of Bray–Curtis dissimilarity index fall between 0, where the two communities are identical and 1, where the two communities are completely dissimilar and share no common species. Based on Bray–Curtis dissimilarity, we further tested for homogenization of the native plant communities by comparing the mean dissimilarity of invaded and non-invaded plots. Because of lack of independence in the data due to each plot being used for n-1 pairwise dissimilarity calculations, we tested for significance of differences in mean dissimilarity between the two groups by a permutation procedure which compared the observed difference in means to 1000 random draws (Jurasinski and Kreyling 2007). Then, non-metric multidimensional scaling (NMDS) (Kruskal 1964) was used to collapse the information of species compositions to two

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**Table 1**  Basic geographical characteristics (average representation per site) of the three sites where the data were collected (Fig. 1). See Online Resource 1 for detailed information of each plot

| Site | Position       | Altitude (m a.s.l) | Slope (°) | Soil depth (cm) | Soil pH | No of plots |
|------|----------------|--------------------|-----------|-----------------|---------|-------------|
| 1    | 15.345N 38.962E | 2395 ± 8           | 15 ± 2.8  | 12 ± 2.5        | 6.3 ± 0.4| 24          |
| 2    | 15.248N 38.762E | 2198 ± 6.6         | 8 ± 1.2   | 8 ± 1.2         | 6.4 ± 0.5| 24          |
| 3    | 15.231N 38.899E | 2245 ± 8           | 9 ± 2.9   | 12 ± 1.9        | 6.4 ± 0.4| 24          |

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Fig. 1 A map of the study area and the three study sites in the highlands of Eritrea
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Dimensions for better visualization and interpretation. Additionally, the significant environmental vectors (elevation, slope and soil depth) were fitted into the ordination space using the function `envfit` in the vegan package. Furthermore, species that were significantly affected in their occurrence by the presence of *O. ficus-indica* were identified with an indicator species analysis (Dufrêne and Legendre 1997) using the `indval` function in labdsv package (version 2.0–1; Roberts 2019). The presence or absence of *O. ficus-indica* was used to differentiate the invaded and control plots. Thus, we excluded *O. ficus-indica* while calculating community composition or species richness. We fitted a linear mixed-effects model and used ANOVA (`lmerTest` package, version 3.1-0; Kuznetsova et al. 2017) to assess the effects of *O. ficus-indica* on species diversity in which the indices of diversity were treated as dependent variables while invasion status of a plot was treated as a fixed-effect independent variable. Plot pair was nested within the study site and treated as a random-effect independent variable. Native species richness and Shannon diversity index were calculated and compared between control and invaded plots in the same way. All statistical analyses were performed in R (version 3.6.0; R Core Team 2019).

**Results**

A total of 45 plant species were identified from 25 families on the 36 pairs of plots (see Online Resource 2). The dominant families were Asteraceae, Lamiaceae, Fabaceae and Solanaceae. In the invaded plots, *O. ficus-indica* reached an average cover of 49% ± 18% (SD). The number of juvenile *O. ficus-indica* increased with the number of adult *O. ficus-indica* (p = 0.026; r^2 = 0.14) and a total cover of *O. ficus-indica* (p = 0.001; r^2 = 0.26), indicating its potential to form dense and lasting thickets once established.

The overall plant species composition between the pairs of invaded and uninvaded plots of the sites differed significantly (ANOSIM: R = 0.24; p < 0.001, Fig. 2). The invasion by *O. ficus-indica* led to a significant homogenization of community compositions (Fig. 3, permutation test: F = 19.6, p < 0.001). The environmental parameters with significant (p < 0.05) link to the plant species composition, in addition to the described effect of invasion by *O. ficus-indica*, were elevation, slope and soil depth of the plots (Fig. 3). This result corresponded well with univariate regressions showing higher cover by *O. ficus-indica* with increasing altitude (p = 0.002; R^2 = 0.23), increasing slope (p = 0.050; R^2 = 0.11) and increasing soil depth (p = 0.005; R^2 = 0.21). The indicator species analysis (see Online Resource 2) revealed that *Plectranthus hadiensis* (p = 0.007) occurred together with *O. ficus-indica* more often, while *Psiadia punctulata* occurred more often in the absence of *O. ficus-indica* (p = 0.041).

The indicator species analysis showed that *Bidens pilosa* (p = 0.10) and *Tagetes minuta* (p = 0.22), which are themselves invasive species, had no significant link to the plots invaded by *O. ficus-indica*. We also checked their role in homogenization of communities by comparing plots where they were present to plots where they were absent. The results based on the subset of sites where the species occurred, *Tagetus minuta* (p = 0.501) and *Bidens pilosa* (p = 0.165) did not exert a significant effect on homogenization.

The species richness (p = 0.311) and Shannon diversity index (p = 0.098) did not differ significantly between the invaded and uninvaded plots. Furthermore, species richness and Shannon diversity were not significantly related to the cover of *O. ficus-indica* (p = 0.226 and p = 0.191, respectively).

**Discussion**

Our results showed that species composition of the plant communities was significantly homogenized by the presence of *O. ficus-indica* while species richness and Shannon diversity were not significantly affected by the presence of *O. ficus-indica*. This suggests that the spread and abundance of *O. ficus-indica* reduce landscape-level heterogeneity or spatial diversity (Jurasiński and Kreyling 2007) of the native plant communities. This finding corresponds well with other studies which have shown homogenization of native plant communities due to invasive species (McKinney 2005; Olden and Rooney 2006; Pino et al. 2009; Qian and Ricklefs 2006). Chen et al. (2013), for example, found that *Solidago canadensis* invasions have resulted in community homogenization across diverse habitats and landscapes which were formerly dominated by different species. They concluded that the community patterns of sites invaded by *S. canadensis*...
were highly similar to each other but dissimilar to those in the control sites, a scenario that corresponds to the homogenizing nature of invasive plants. The ability to form homogenous stands, which is typical for *O. ficus-indica*, appears to drive the interference with the native species (Zimmermann et al. 2009). It has previously been reported that invasions can have a limited effect on species richness of communities (Hejda and Pýšek 2006). However, changes in species composition can occur and native, fast-growing species can increase in abundance in the invaded communities. Accordingly, we found *Plectranthus hadiensis*, a semi-succulent fast-growing herbaceous plant to occur more frequently with *O. ficus-indica*. On the other hand, *Psiadia punctulata*, a drought-resistant East African shrub was found to avoid the presence of the invasive plant. It is reported that *P. punctulata* is usually avoided by some herbivore animals even during severe drought conditions. An exudate, rich in pharmacologically active secondary metabolites, is potentially responsible for its unpalatable nature and drought resistance (Midwo et al. 2003; Juma et al. 2001; Juma et al. 2006). We thus hypothesize that one important impact of the presence of *O. ficus-indica* on native diversity occurs

Fig. 2 The difference in species compositions between invaded and non-invaded plots graphically visualized by non-metric multidimensional scaling (NMDS). Statistics stem from an analysis of similarity (ANOSIM) based on Bray–Curtis dissimilarity with final two-dimensional stress of 0.23. Species occurrence in the ordination and significant environmental parameters depicted in blue are shown for the same ordination in the second panel. See Online Resource 2 for the full species list

Fig. 3 Invasion by *O. ficus-indica* led to the homogenization of native plant community compositions as indicated by a decrease in mean Bray–Curtis dissimilarity. Displayed are the mean ± 1 SE of all pairwise Bray–Curtis dissimilarities per group. Significance of the differences between the invaded and adjacent uninvaded plots was tested using a permutation test with 1000 permutations.
through affecting grazing and browsing patterns by herbivores. *Opuntia ficus-indica* likely shelters species sensitive to herbivory and competes with browsing-tolerant species for space, presumably explaining that its presence showed no significant impact on native species diversity and richness. These results imply that the impact of the invasive *O. ficus-indica* on the diversity and richness of native vegetation may be lower than previously thought. A similar situation was reported from Kenya (Oduor et al. 2018) where a similar study was performed by surveying the native vegetation in Nairobi National Park between *O. ficus-indica* invaded and uninvaded sites. They found that communities invaded by *O. ficus-indica* had significantly higher native species richness and diversity because *O. ficus-indica* sheltered the native species against grazing.

A potential drawback of observational studies comparing invaded and uninvaded habitats is that they may be biased by the fact that species diversity in itself can affect the likelihood of invasion, which makes it difficult to separate cause and effect (Hejda and Pyšek 2006; Levine and D’Antonio 1999; Hulme and Bremner 2006). However, since our results showed no difference in species diversity between invaded and uninvaded communities, the prediction that species-poor stands could have been more easily invaded is irrelevant to our study (Hejda and Pyšek 2006). Quantitatively measuring the impacts of invasive species on native communities in the field is difficult. This is because invasion is a long-term process rarely observed from the time of the introduction and establishment of the invasive species (Müllerová et al. 2005). We used the invaded and uninvaded plots to overcome this difficulty. The uninvaded plots represented the native vegetation before the invasion occurred (Pyšek and Pyšek 1995) which justifies the ‘space for time’ substitution approach that is often used in studies on vegetation succession (Alvarez and Cushman 2002; Badano and Pugnaire 2004; Ruprecht 2005). The measurements of the species diversity between the invaded and uninvaded plots were then used in quantitively assessing the species richness, diversity and composition of the vegetation.

In its regions of origin, *O. ficus-indica* is found at elevations of over 4700 m (Nobel 1994) or in the introduced areas such as South Africa and Australia in highlands above 2000 m (Johnson 1982; Zimmermann and Moran 1991; van Sittert 2002). It is thus well-fitted to grow in high altitudes, and in our study area at the Eritrean highlands, it grows vigorously and is abundant at elevations around 2000 m. It is a common conception that *O. ficus-indica* is planted for soil conservation and prevents erosion at steep slopes and higher altitudes (Bein et al. 1996), and we thus expected to find it primarily in those habitats. With respect to the effect of the environmental parameters on invasibility, higher cover and invasion success occurred in steeper and higher sites than in flatter sites or at lower elevations. Erre et al. (2009) studied the distribution of *O. ficus-indica* in the Mediterranean Basin and on the contrary found that the invasive plant was not common at higher altitudes due to the low temperatures in the region. The cover of *O. ficus-indica* also tended to increase with increasing soil depth. This could be attributed to the government’s efforts to prevent soil erosion by terracing the landscape in higher altitudes with steep slopes which eventually conserved the soil and resulted in higher soil depths.

The successful establishment of *O. ficus-indica* depends on its unique biological traits and the environmental characteristics of the ecosystems it invades. It is suggested that the fluctuation in resource availability makes plant communities susceptible to invasion (Davis et al. 2000). Water availability in dry climates displays an example for this theory, as temporal fluctuations cause intermittent lack of resource availability, followed by water availability upon rainfall. This pulsed regime of water availability can make communities vulnerable to drought-tolerant invasive specialists such as *O. ficus-indica*. Its invasion success may consequently be amplified by climate change, which leads to warmer and drier conditions in the study area (Funk et al. 2015; Serdeczny et al. 2017) and can be expected to further increase the competitive ability and thereby the invasiveness of *O. ficus-indica* as it originates from even warmer and drier conditions (Novoa et al. 2015). To better project the future invasive potential of *O. ficus-indica*, controlled competition experiments with *O. ficus-indica* and native plants are needed.

Our data show that invasion by *O. ficus-indica* leads to plant community homogenization in the Eritrean highlands. While species richness and diversity appear unaffected by this invasion, homogenization is another negative consequence. Successful recruitment and
densification of established *O. ficus-indica* stand suggest an intensification of this problem in future, likely exacerbated by climate change and further enhanced by the lack of awareness of the local communities on the impacts of its invasion (Ogbazghi and Stillhardt 2011). The nurturing of the plant for different local uses (e.g., hedging, fodder, edible fruits) utilizing its drought-tolerant nature increases the potential for further spreading of this invasive species (Bein et al. 1996) and the interference with the spatial diversity and ecosystem processes of the native vegetation. It will likely become a long-term dominant species with an increasing impact on the native vegetation. The real challenge now lies in raising the local awareness of the issue and preventing further spread of the species to other natural ecosystems.

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