Nature Conservation 24: 1–20 (2018)
doi: 10.3897/natureconservation.24.20942
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Proposed biodiversity conservation areas: gap analysis and spatial prioritization on the inadequately studied Qinghai Plateau, China

Renqiang Li[1], Ryan Powers[2], Ming Xu[3], Yunpu Zheng[4], Shujie Zhao[5]

1 *Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources, the Chinese Academy of Sciences, 11A Datun Road, Beijing, 100101, China* **2** *Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven 06520, CT, USA* **3** *Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA* **4** *School of Water Conservancy and Hydropower, Hebei University of Engineering, Handan 056038, China* **5** *Central University of Finance and Economics, 39 South College Road, Beijing, 100081, China*

Corresponding authors: *Renqiang Li* (renqiangli@igsnrr.ac.cn); *Ming Xu* (mingxu@crssa.rutgers.edu)

Academic editor: *C. Margules* | Received 12 September 2017 | Accepted 4 December 2017 | Published 4 January 2018

http://zoobank.org/D94DE26F-1CC5-455A-83ED-5BA02B923C34

Citation: Li R, Powers R, Xu M, Zheng Y, Zhao S (2018) Proposed biodiversity conservation areas: gap analysis and spatial prioritization on the inadequately studied Qinghai Plateau, China. Nature Conservation 24: 1–20. https://doi.org/10.3897/natureconservation.24.20942

Abstract

Global biodiversity priorities are primarily addressed through the establishment or expansion of conservation areas (CAs). Spatial prioritization of these CAs can help minimize biodiversity loss by accounting for the uneven distribution of biodiversity and conservation considerations (e.g., accessibility, cost, and biodiversity threats). Furthermore, optimized spatial priorities can help facilitate the judicious use of limited conservation resources by identifying cost effective CA designs. Here, we demonstrate how key species and ecosystems can be incorporated into systematic conservation planning to propose the expansion and addition of new CAs in the biodiversity-unique and data-poor region of Qinghai Plateau, China. We combined species distribution models with a systematic conservation planning tool, MARXAN to identify CAs for biodiversity on Qinghai Plateau. A set of 57 optimal CAs (273,872 km^2, 39.3 % of this Province) were required to achieve the defined conservation targets in Qinghai Province. We also identified 29 new CAs (139,216 km^2, 20% of Qinghai Province) outside the existing nature reserve (NRs) that are necessary to fully achieve the proposed conservation targets. The conservation importance of these 29 new CAs was also indicated, with 10 labeled as high priority, 11 as medium priority, and 8 as low priority. High priority areas were more abundant in the eastern and southeastern parts of this region. Our results suggest that many species remain inadequately protected within the Qinghai Plateau, with conservation gaps in eastern and northwestern regions. The proposed more representative and effective CAs can provide useful information for adjusting the existing NRs and developing the first National Park in China.

Keywords

Conservation planning, conservation area, Qinghai Plateau, spatial prioritization, species distribution model

Introduction

The massive growth in the human population and rapid land-cover change has led to unsustainable exploitation and use of biodiversity resources, exacerbated by climate change, biological invasion and other environmental influences (Rands et al. 2010; Alroy 2015; Luo et al. 2015; Chen et al. 2017). Human-induced environmental changes has caused the sixth extinction of 5–20% species in many biological groups, and scientists estimate that we are now losing species at 100–1,000 times greater than pre-human rates (Pimm et al. 1995; Chapin et al. 2000; Lawton et al. 2005). In order to effectively address human and other environmental impacts on biodiversity, conservation areas (CAs) are widely considered essential for managing species habitats and enhancing ecosystem services (Liu et al. 2003; Carranza et al. 2014; Gray et al. 2016; Zhang et al. 2017). Recognition of this imperative has resulted in the protection of around 15% of Earth's land and 3% of the oceans (Andrew et al. 2012; Gray et al. 2016). However, there is no consensus on the effectiveness of CAs as a conservation tool, and substantial conservation gaps still exist, leaving much the world's remaining biodiversity unprotected (Laurance et al. 2010; Gray et al. 2016).

Most of conservation policies worldwide focus overwhelmingly on expanding the coverage of CA networks to achieve conservation targets. In 2010, 193 parties of the Convention of Biological Diversity (CBD) recommended a new strategic plan to combat global biodiversity decline. A key element of this plan is Aichi target 11, which includes a commitment to expand the global coverage of CAs to at least 17% of terrestrial land and 10% of marine areas by 2020 (Aichi Target 11, CBD 2011; Sanderson et al. 2015). CBD targets, if adhered to, have the potential to spur rapid worldwide expansion of the CA networks (Watson et al. 2014). However, the CA's size does not guarantee desirable conservation outcomes; its effectiveness also depends on where it is located. Thus, there has been a critical need for the strategic expansion of CA networks (Venter et al. 2014). It is important to acknowledge that the planning of CAs is typically understaffed, underfunded, and beleaguered in the face of external threats, so conservation efforts should also be complemented with the appropriate management and planning of existing CAs (Sanderson et al. 2015). Previous calls for enhancing CA management have focused on improving operational effectiveness of each CA. However, little guidance has been offered on how to increase the collective effectiveness for meeting biodiversity conservation goals and improving the performance of CAs (Sanderson et al. 2015).

Species distribution models (SDMs), also commonly referred to as ecological niche models (ENMs), have become a fundamental tool used to spatially predict habitat suitability in ecology, biogeography, and conservation biology (Franklin 2013; Guisan et al. 2013). These SDMs, which rely on ecological theory of processes that mediate species distributions and abundance – especially niche theory (Guillera-Arroita et al. 2015), are currently the main approach for converting individual point-locality data, such as museum collection records (Loiselle et al. 2003; Peterson et al. 2011) into the potential distributional range of a species or predicted ranges following global climate change (Li et al. 2015). Thus, SDMs have the potential to play a critical role in supporting spatial conservation decision making, especially when conservation biologists are often pressed to make recommendations about conserving biodiversity based on limited species-distribution data and biodiversity resources (Addison et al. 2013).

Conservationists may aspire to protect as much of the Earth's remaining biodiversity as possible, but limited conservation resources beget the need for spatial prioritization or the placement of CAs in areas that maximize the greatest return on investment (Carwardine et al. 2009). Systematic conservation-planning approaches help support the judicious use of conservation resources by identifying potential areas that efficiently meet specified conservation targets for the least cost (Margules and Pressey 2000; Carwardine et al. 2008; Linke et al. 2012). In general, systematic conservation approaches also aim to identify priority areas or refugees for ensuring the representation and long-term persistence of biodiversity (Margules et al. 2002; Leslie et al. 2003; Wu et al. 2011; Hermoso and Kennard 2012), and usually include multistep procedures, (1) choosing a set of conservation features (species, ecosystems, or ecosystem services) as surrogates of biodiversity in a region, (2) defining the targets for each of these conservation features, and identifying the conservation gap, (3) assigning a conservation cost to each planning unit in a region, and (4) using conservation planning software to identify priority areas for biodiversity based on meeting the defined conservation goals, increasing landscape connection, and minimizing conservation cost (Fajardo et al. 2014).

Qinghai Province is located in the Qinghai-Tibet Plateau, a globally unique biogeographic area. It has one of the highest concentrations of biodiversity among the high altitude regions in the world, and has also been classified as area of high conservation importance by the Chinese government. To date, the Qinghai Province has established 11 NRs, with a total area of 218,000 km^2, covering 30.2% of the province's land area. Importantly, however, these NRs are reputed to be biased to less economically viable areas (i.e., minimal foregone resource opportunities). Since representation of biodiversity did not drive the selection of these NRs, many species and habitats remain inadequately protected and vulnerable to threatening processes. Due to the lack of biodiversity information, the effectiveness and representation of species conservation in this region has not been systematically explored. Moreover, China is planning the world's biggest National Park in the Qinghai-Tibet Plateau, which is the first National Park in China and will cover some 120,000 square kilometers. The identification of the National Park's boundary represents a substantial challenge to its development. The goals of this study are to: (1) evaluate the ability of existing NRs to contribute to the overall goal of protecting key species and ecosystems; (2) identify a set of CAs that meet our defined conservation targets, and (3) prioritize these additional CAs outside of the existing NRs in Qinghai Province to provide important information for the creation of National Park.

Materials and methods

Study area

Qinghai Province is situated in the northeast of the Qinghai-Tibet plateau, which is the “water tower” of China and Asia (Huang 2013). Its total area is 7.2×10^4 km^2, one thirteenth of China’s total area. It comprises the headwaters of several major Asian rivers, including the Yellow, Yangtze, Mekong, Salween and Yarlung Tsangpo (Brahmaputra) rivers, and thus contributes significantly to the livelihood and wellbeing of nearly 40 percent of the world’s population. Therefore, it is important to conserve this region for the livelihoods of all those people. The elevation in the province ranges from 1664 m to 6619 m (Fig. 1). From extensive alpine grasslands and wetlands to forests and deserts, Qinghai is home to a wide variety of globally significant, but fragile ecosystems. As a traditionally sparsely inhabited region with a variety of different climatic zones and natural habitats, Qinghai Province provides important habitats for many endangered species including the Tibetan antelope, wild yak, argali, snow leopard, black necked crane, saker falcon and many other key endangered wild animals.

Conservation features

Efficient expansion of CAs requires simultaneous planning for species and ecosystems (Polak et al. 2015). Qinghai Forestry Department put forward a list of 79 rare and endangered species in 2013 as indicator species of biodiversity conservation in Qinghai Province. We thus used 11 endemic ecosystem types (Table 1) and 72 of the 79 endangered species (Table 2) as the surrogate of biodiversity in this region. In this study, we integrated conservation features from three sources to achieve maximum representation of biodiversity and compensate for limitations in data availability: (1) China key rare and endangered species database collected by The Nature Conservancy’s China biodiversity blueprint project. This database has been successfully used to predict climate change induced range shifts of *Galliformes* in China (Li et al. 2010). It was once employed to identify conservation priority areas in “China national biodiversity conservation strategy and action plan (2011–2030)” (Ministry of Environmental Protection 2010); (2) Chinese Endangered Species Information System (CESIS) (Xie et al. 1997). This system collected the latest endangered species information including mammals, birds, reptiles, amphibians, fish species or subspecies in China. Both the theoretical and practical simulations show that when the number of species presence

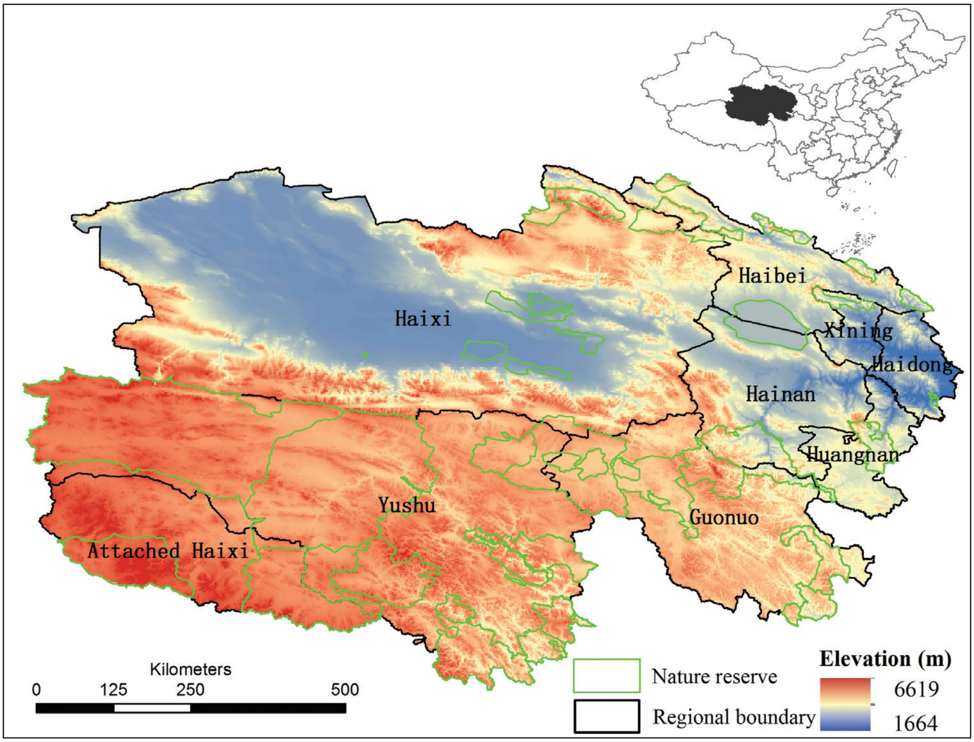

Figure 1. The location of Qinghai Province in China and the elevation range.

points is greater than 14, the species distribution model can produce a better simulation result of species habitat (Proosdij et al. 2015). Therefore, we excluded these species with less than 15 presence points from the two databases, and obtained species presence data for 59 key rare and endangered species (Table 2). We checked the independence of the records and used them to input species distribution models to simulate their geographic ranges; (3) We identified the other 13 species' suitability range using expert range maps from the online IUCN website (Table 2).

Species distribution modelling

We applied a maximum entropy modelling technique with the MAXENT software (Phillips et al. 2006) to predict the graphic distributions of the 59 endangered species. This approach has been extensively adopted to project species range shifts and change in species diversity patterns and to inform conservation planning (Hernandez et al. 2008; Costa et al. 2010; Ponce-Reyes et al. 2012; McPherson 2014). A set of 19 bioclimatic variables at 30s resolution were collected from the WorldClim dataset for current conditions (average for 1951–2000) (Hijmans et al. 2005). We performed a principal components analysis of 19 bioclimatic variables to select the first three principal com-

Table 1. Conservation targets for regional endemic or endemic ecosystems to China in Qinghai Province.

Vegetation name	Endemism	Conservation target (%)
Carex moorcroftii Steppe	Regional endemic	15
Kobresia humilis Alpine meadow	Regional endemic	15
Alpine kobresia Meadow	Regional endemic	15
Kobresia capillifolia Alpine meadow	Regional endemic	15
Populus euphratica Forest	Regional endemic	10
Picea balfouriana Forest	Endemic to China	10
Picea purpurea Mast Forest	Endemic to China	10
Picea asperata var. *ponderosa* Forest	Endemic to China	10
Abies fabri (Mast.) Craib	Endemic to China	10
S. convallium Forest	Endemic to China	10
Qinghai spruce Forest	Endemic to China	10

Table 2. Summary of species data source, the proposed conservation goal of each species according to their current conservation status, spatial distribution size and endemic status, and species representation (percentage protected) in the current nature reserve network of Qinghai Province based on the conservation goals defined in this study.

Scientific name	Record points	Target (%)	Percentage protected (%)
Pseudois nayaur	183	5	40
Gypaetus barbatus	52	5	36
Ithaginis cruentus	85	5	35
Tetraogallus tibetanus	55	15	41
Aquila heliaca	34	20	44
Otocolobus manul	144	5	29
Moschus chrysogaster	116	15	33
Mustela altaica	171	10	26
Crossoptilon auritum	72	10	25
Lynx lynx	269	7	22
Martes foina	140	5	19
Tetraogallus himalayensis	43	6	19
Gervus albirostris	195	20	32
Grus nigricollis	111	20	32
Marmota himalayana	95	5	17
Buteo hemilasius	179	13	21
Haliaeetus leucoryphus	75	15	23
Bos mutus	104	25	32
Equus kiang	79	25	32
Pantholops hodgsonii	133	25	32
Ailurus fulgens	319	34	37
Falco cherrug	48	29	32
Pandion haliaetus	77	24	26
Procapra picticaudata	123	33	33
Ovis ammon	130	17	17

Scientific name	Record points	Target (%)	Percentage protected (%)
Aegypius monachus	225	16	15
Canis lupus	506	23	22
Panthera uncia	161	30	28
Bonasa sewerzowi	31	27	25
Gyps himalayensis	96	19	17
Antropoides virgo	105	11	8
Cygnus olor	41	13	10
Capricornis rubidus	504	28	24
Ursus thibetanus	225	29	24
Grus grus	110	14	9
Cervus unicolor	318	31	25
Accipiter nisus	297	35	27
Lophophorus lhuysii	47	39	30
Aquila nipalensis	105	21	11
Gazella subgutturosa	94	16	4
Cygnus cygnus	128	18	6
Falco peregrinus	77	23	9
Cervus elaphus	246	39	25
Lutra lutra	552	28	14
Falco subbuteo	91	25	11
Ciconia nigra	277	24	9
Milvus lineatus	344	23	6
Falco tinnunculus	248	25	8
Otis tarda	122	24	5
Cuon alpinus	207	31	11
Chrysolophus pictus	503	28	8
Pelecanus onocrotalus	16	23	3
Mustela sibirica	573	25	4
Vulpes vulpes	718	25	3
Macaca mulatta	653	30	5
Panthera pardus	425	49	21
Neofelis nebulosa	292	35	0
Andrias davidianus	185	54	1
Strix uralensis	Range map	25	100
Circus cyaneus	Range map	5	32
Bubo bubo	Range map	5	32
Athene noctua	Range map	5	32
Ursus arctos	Range map	5	31
Accipiter nisus	Range map	7	25
Aquila chrysaetos	Range map	12	29
Procapra przewalskii	Range map	60	68
Moschus berezovskii	Range map	29	33
Haliaeetus albicilla	Range map	18	13
Asio otus	Range map	23	14
Felis bieti	Range map	29	19
Platalea leucorodia	Range map	24	0

ponents as input climatic variables for our SDMs. We also included vegetation types and two human disturbance factors (population density and gross domestic product) into model input layers.

MAXENT was run in default settings with a maximum of 500 iterations. We used cross-validation procedures to model calibration, which randomly assigned 75% of species records while keeping the other 25% records for AUC computations. We assessed model performance with AUC, which provides a single measure of model performance and ranges from 0.5 (randomness) to 1 (perfect discrimination), where a score higher than 0.7 is considered a good model performance (Rebelo et al. 2010). Outputs from MAXENT models were reclassified to presence/absence predictions using the "Maximum Training Sensitivity Plus Specificity" threshold, which has proven to generally produce more accurate results than other thresholds (Fajardo et al. 2014; Liu et al. 2005).

The targets of conservation features

We defined conservation targets for each species according to the current conservation status, spatial distribution range and endemic status (Fajardo et al. 2014). The target for each species was calculated as the sum of the following three indices: conservation status index, distribution size index, and conservation endemic index.

Distribution size index: Species with smaller distribution area should have a higher conservation priority and target, whereas species with larger distribution area should have lower a conservation target (Rodrigues et al. 2004). We assigned a more demanding representation target to species with more restricted ranges, acknowledging the negative relationship between species distribution size and extinction risk (Gaston and Rodrigues 2003). The value given to each species was scaled between a minimum coverage of 5% for species with a distribution equal to or greater than 300,000 km^2 in Qinghai Province, and a maximum of 25% for species with ranges equal to or less than 1,000 km^2 (Rodrigues et al. 2004). The 300,000 km^2 upper threshold corresponds to the range size observed in one third of the studied species in Qinghai Province.

Conservation status index: Like in Fajardo et al. (2014), we assigned goals to species identified as threatened by the IUCN following a decreasing scale: Critically Endangered (CR), 25%; Endangered (EN), 17.5%; Vulnerable (VU), 10%; Near Threatened (NT), 5%; Least Concern (LC), Not Evaluated (NE), and Data Deficient (DD), 0%.

Conservation endemic index: An endemic species is one whose habitat is restricted to a particular area, and can be easily under threat. As such, endemic species are of great conservation interest to conservation planning. We assigned goals of 10% for species endemic to Qinghai-Tibet Plateau, 5% for endemic species in China, and 0 for other species.

In Qinghai Province, wetland, forest and endemic grassland ecosystems have high conservation importance. Existing NRs already protect 70% of the important plateau wetland ecosystem (Liu and Li 2007). Therefore, we exclusively focused on endemic grassland and unique forest ecosystems. We used vegetation map of China (1:1 000 000) to represent ecosystem features of this region, and selected 11 endemic vegetation types as key conservation ecosystem types according to their endemism in this region or China (Qu 2011). We identified their conservation target as 10% for ecosystems endemic to the Qinghai-Tibet Plateau, 5% for endemic ecosystems in China, and 0 for other ecosystems. Although the conservation targets were determined arbitrarily, the results from our scenarios indicated that the changed conservation targets for each conservation feature did not radically affect the spatial distribution of the proposed CAs.

Species representation within the existing nature reserves

We performed a gap analysis that compared the defined conservation targets to species' current representation within existing NRs. The species distributions and expert range maps were first intersected with the NRs, and then the percentage of its distribution within NRs was calculated and compared with its defined conservation targets. Species are considered insufficiently protected by the current NRs when the percentage is below their conservation targets.

Proposed conservation priority areas

We used the systematic conservation planning software MARXAN 2.4.3 (Ball et al. 2009) to identify the most efficient set of conservation priority areas to meet the above targets for both ecosystems and endangered species. It is a decision-support tool, which solves an optimization problem of representing a set of conservation features (species, ecosystems, ecoregions or ecosystem services) at a minimal cost, and has been widely used for identifying CAs in China (Wu et al. 2014; Zhang et al. 2014) and across the world (Powers et al. 2013; Hermoso et al. 2013; Tulloch et al. 2016; Powers et al. 2016). The Qinghai Province was partitioned into 4 km × 4 km grids or 44,475 planning units (PUs). We unlocked Kekexili National NR and the Soka River Protection zone of Sanjiangyuan National NR, the two largest NRs of current network, and set PUs in them as "available", because we assumed that the large extent of these two NRs may not be required to effectively meet conservation targets. PUs coinciding with other current NRs were prioritized in the MARXAN solutions. We set the cost of each PU as the value of the human footprint index (Sanderson et al. 2002). This index assumed that PUs with less human disturbance have higher social acceptance (Powers et al. 2013) and a lower conservation cost, and is widely accepted as a universal conservation cost surrogate (Fajardo et al. 2014; Wu et al. 2014). We ran different scenarios using the Zonae Cogito Decision Support System to test the most suitable parameters for MARXAN whereby we varied the boundary length modifier (BLM) and the species penalty factor (SPF). BLM and SPF were optimized to 100 and 1 respectfully since it offered an efficient tradeoff in our scenario analysis between cost, reserve compactness and achieving conservation targets. We ran MARXAN to identify 100 solutions using the simulated annealing algorithm and the default values for number of iterations (1,000,000) and temperature Decreases (10,000).

The best solution from the MARXAN output is the network most optimized with respect to achieving the conservation targets at the lowest cost. We thus proposed priority areas from MARXAN's best solution. Given the financial challenges associated with the immediate implementation of these areas proposed in the best solution, we prioritized the areas outside of existing NRs according to three important decision making criteria: species richness, selection frequency, and vulnerability. Species richness was generated by calculating the number of studied species present in each 4 km×4 km grid cell across the entire study region based on the binary distribution maps from species distribution models and the range maps. It has long been recognized as a key characteristic determining biodiversity patterns and conservation selection. The grid cells with higher richness were assumed to have higher conservation value and were preferentially prioritized. MARXAN produced 100 solutions and a summed solution made up of the selection frequency across the 100 runs. This score of selection frequency represents the total section frequency of each grid. The vulnerability criteria is used to prioritize highly impacted areas that are in greater need of protection. We should give priority to protecting areas where human disturbance is more serious and ecologically more sensitive. To calculate the score, we used the human footprint index as a measure of the human influence on each PU.

The three criteria scores were normalized to values between 0 and 100, and summed to give each proposed CA an overall priority score. Priority areas were classified as high, medium, and low priority according to the overall priority score. The area of high, medium, and low priority was determined using natural break method (Fajardo et al. 2014).

Results

Spatial patterns of species richness in Qinghai Province

The species distribution models were able to accurately predict the geographic distributions of the species. Specially, the models had AUC values between 0.843 and 0.999, which indicates that the generated geographic distributions can be used to estimate regional species richness patterns and conservation planning (Fig. 4a). Species richness was spatially heterogeneous and follows the well-known latitudinal pattern in Qinghai Province. Its spatial pattern shows a general reduction from the eastern to western areas. The maximum value of 57 species per km^2 is located in the Haidong and Xining regions. Regions with a relatively low number of species are situated in the western high altitude areas, including Haixi and Yusu (Fig. 4a).

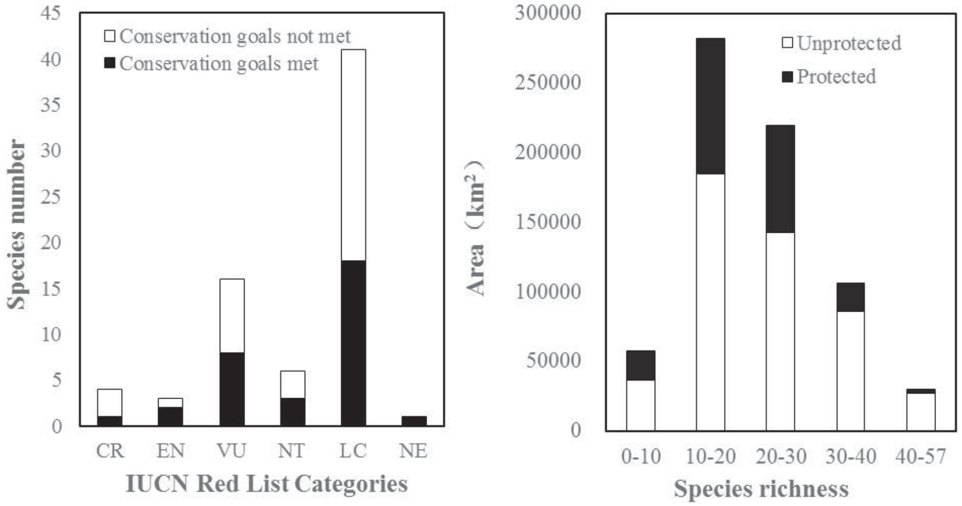

Figure 2. Summary of the conservation gap for key rare and endangered species in Qinghai Province: (a) species number of conservation goals met and not met; (b) the area protected and unprotected in nature reserves (CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC - Least Concern).

Conservation effectiveness in the current NRs

The 11 NRs account for 30.2% of the total Qinghai Province area. The percentage of area with 10–20 and 30–40 species/km^2 protected by the current NRs was 37% and 35%. The two regions with the highest species richness encompassed an area of 110000 km^2 and 3000 km^2 respectively, and had a low protection level of 19% and 11% (Fig. 1). These two regions are mainly located in the farming-pastoral ecotone within the eastern and southern parts of Qinghai Province.

We found that 41 species, 53% of the total, are insufficiently protected in the current reserve system according to our defined conservation target for each species. We also found that targets for those species most at risk species are not well met under current NRs: 3 out of 4 critically endangered, on third of the endangered, and 8 out of 16 vulnerable species did not achieve their defined conservation goals (Fig. 2). There were 22 and 11 species whose protection under existing NRs exceeded conservation targets by 10% and 20% respectively (Fig. 2).

Proposed priority areas for biodiversity conservation

A set of priority areas based on the best solution were selected in Qinghai Province (Fig. 3). We identified 57 optimal CAs for biodiversity conservation in Qinghai Province. The total area assigned as CAs in order to achieve the conservation targets for all conservation features is about 273,872 km^2, about 39.3 % of the total land area

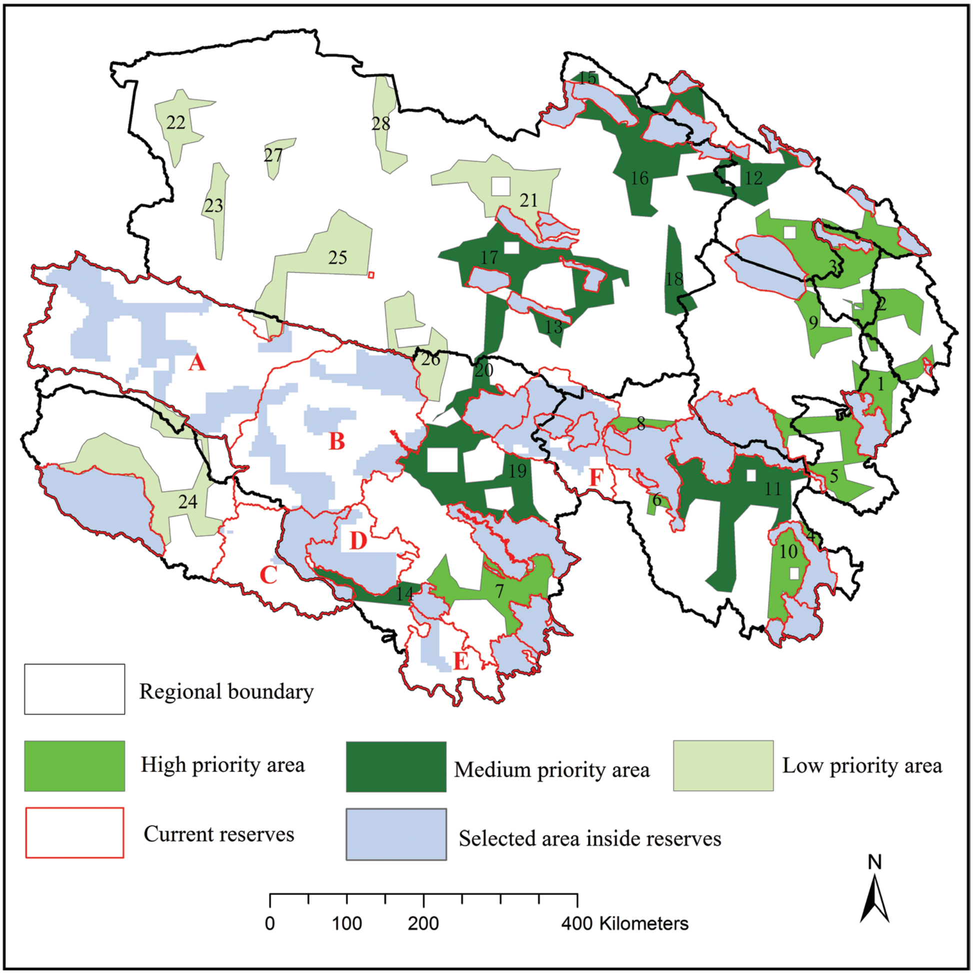

Figure 3. Spatial distribution of proposed priority areas (including high, medium and low priorities) inside and outside the existing nature reserves for Qinghai Province.

in Qinghai Province. Among these selected priority areas, 28 areas are located within the existing NRs. The total area of selected CAs inside current reserves is about 134,656km^2, 19.3% of Qinghai Province. In order to better guide conservation investment and management, we judiciously reduced the coverage of the Sanjiangyuan National NR (conservation zone A, B, C and D in Fig. 3). This very large protected area was not optimized; therefore, its conservation effectiveness (e.g., reduced conservation cost, greater transparency and objectiveness, and higher level of protection for more species) can be improved by systematic conservation planning.

To fully meet our criteria for our conservation features, 29 new or not previously conserved areas, approximately 139,216 km^2 (20% of Qinghai Province), were added to the current NR system (Fig. 3). The majority of these new conservation priority

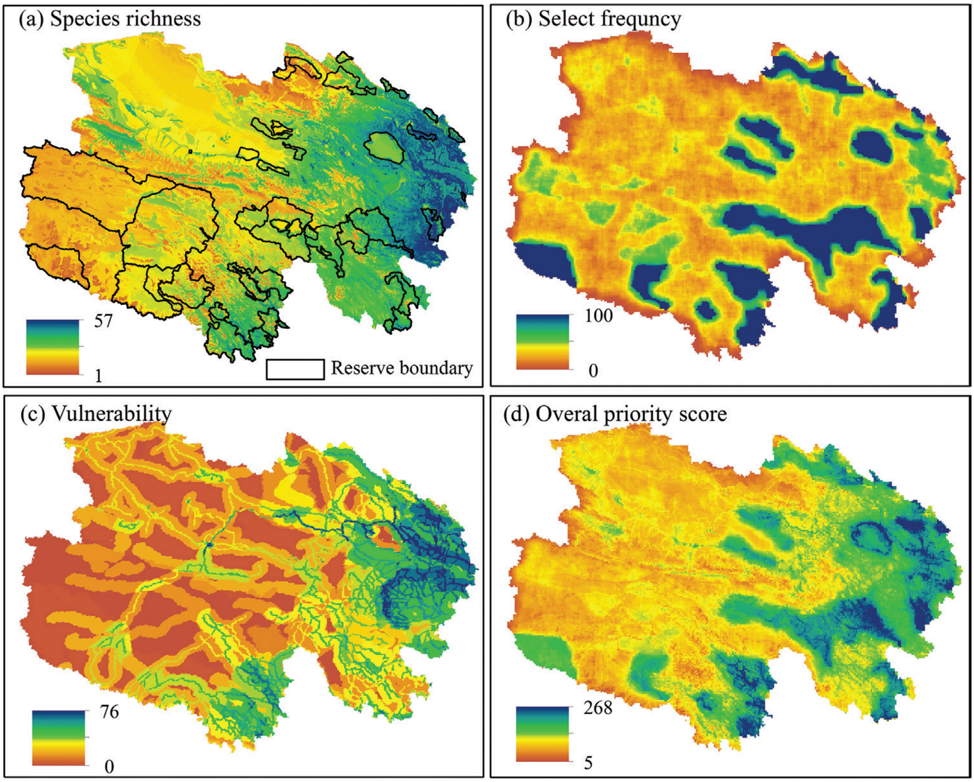

Figure 4. Spatial distribution maps for the three criteria used to evaluate the conservation priority of the proposed conservation areas in this study: **a** species richness and current nature reserves across Qinghai Province **b** vulnerability, derived from the Human Footprint index **c** selection frequency of the planning units, including additional solutions with varying conservation goals; and **d** overall priority score.

areas were located in the Qinghai Province's east and, to a lesser degree, in parts of the central and southern regions. Some conservation priorities were selected to improve the connectivity among other conservation areas, which were located between Qinghai Qaidam Haloxylon ammodendron forest national NR and Qinghai Nuomuhong Provincial NR (13, 17, and 20 in Fig. 3), Protection Zones of Sanjiangyuan National NR (7 and14 in Fig. 3), and Protection Zones of Qilian Mountain National NR (12 and 16 in Fig. 3).

The prioritization of additional conservation areas

The prioritization of new selected areas outside the existing NRs was determined according to an overall priority score derived from three design criteria: species richness, selection frequency, and vulnerability. The vulnerability of the proposed priority areas, as measured by the vulnerability score, increases gradually from east to west. Of the

29 new areas, 10 were designated as high priority, 11 as medium priority, and 8 as low priority (Fig. 3). High priority areas are more abundant in the eastern and southeastern parts of this province. In general, five additional priority areas were larger than 1000 km^2, while 11 are larger than 5,000 km^2 in size. For the top five largest priority areas, two are in the northeastern region, while three are in the south of Qinghai Province. The largest one (24 in Fig. 3) was the attached Haixi in the southwest of Qinghai (11135 km^2). The second largest (11 in Fig. 3) was in the central part of Guoluo (106906 km^2), the third (19 in Fig. 3) was in the east of Yusu (9989 km^2), while the fourth (3 in Fig. 3) and the fifth (16 in Fig. 3) are located in between Haibei and Xining (9802 km^2) and between Haibei and Haixi (9437 km^2), respectively.

Discussion

To the best of our knowledge, the work described here, is the first time a systematic approach to biodiversity conservation planning has been devised for the Qinghai Province. Our approach focused on the conservation of both species and ecosystem-level features, and builds upon the current NR network to highlight new areas for protection. Other similar studies have demonstrated that, when expanding existing NRs, fewer resources and less land are required to achieve conservation targets if species and ecosystem conservation features are addressed at the same time (Lombard et al. 2003; Polak et al. 2015). By avoiding the selection of planning units that become redundant once a secondary goal is added, the simultaneous inclusion of multiple conservation feature types can lead to final CA solutions that are likely smaller and less costly. Complementarity is a key consideration when planning for conservation (Watson et al. 2008), and assessing this complementarity for Qinghai Province could potentially inform planning for expanding and improving the current conservation system. Our results show the biodiversity conservation gap and spatial distribution of key conservation areas within the Qinghai Province, and can provide an important basis for the assessment and adjustment of regional conservation planning in the future.

The existing and extensive NR network in Qinghai Province plays an important role in maintaining unique endangered species and key ecosystems. However, our results suggest that additional protection is still required. First, the eastern and southeastern parts of Qinghai Province are key areas for biodiversity conservation. These areas are rich in rare and endangered species distributions, but are currently under protected. Further, in many instances the largely unprotected areas surrounding high population densities may warrant additional conservation emphasis, despite greater risks for land-use conflict and implementation challenges, as they typically contain greater diversity, species of concern and have the potential to constrain environmental impacts associated with human activities. New NRs are also recommended for the Qaidam basin of Haixi Mongolian Autonomous Prefecture, which contains no NRs and is home to many species of high conservation value that are unique to these desert ecosystems. In addition, we recommend that the boundaries of some current NRs be adjusted according to the distribution of conservation features. Considerable conservation gains can be achieved if the NR boundaries of Sanjiangyuan Tongtianhe protection division, Angsai protection division, and Mengda and the Xianmi NR are modified to improve the conservation efficiency.

Expanding the proportion of land protected will not guarantee the improvement of conservation effectiveness and representation, and could prove extremely costly. A systematic conservation approach, such as the one presented in this study, provides a useful framework that can help guide planners as to where (spatially) conservation efforts should be targeted to efficiently achieve conservation objectives. Over the last two decades, the number and area of NRs have greatly increased in China. In 2014, there were 2,729 NRs, accounting for about 15% of China's land territory, ann more than 30.2% in Qinghai. Since NRs hold the majority of the country's wildlife, they play a fundamental role in protecting regional biodiversity. Nonetheless, many threatened species are still not adequately protected. Key biodiversity areas, which are the most important sites for biodiversity conservation, are also poorly represented in existing NRs. The effectiveness of many NRs in China is compromised by lack of ongoing financial and technical support, systematic planning and an adequate conceptual base to optimize the conservation performance. The NR system faces serious challenges. We need to act quickly to shift the focus of the construction and management of NRs from quantitative growth to quality improvement, and incorporate systematic planning into conservation practices, because global change and other threats are quickly eroding biodiversity. Unless this is done, we risk many NRs becoming "paper parks"— existing in name only (Di and Toivonen 2015).

Designing and complementing conservation networks to safeguard biodiversity is a difficult task for governments and conservationists in a plateau due to the absence of information regarding species distributions, density or abundance. In this study, we adopted species distribution models (SDMs) to simulate the ranges of key rare and endangered species. These species are largely considered the best available proxy of biodiversity in Qinghai Province. SDMs are increasingly proposed to support conservation decision making, and have the potential to better bridge theory and practice, and contribute to improve both scientific knowledge and conservation outcomes when the ecological knowledge is incomplete, such as in Qinghai plateau. Although the set of 72 key endangered species used in this study as indicator species is not exhaustive and not devoid of uncertainty, the high consistency of our overall results suggest that they are consistent with currently described biodiversity patterns in Qinghai Province. Looking forward, the funding and capacity for collecting more adequate species data and keeping them up to date are critical to future conservation efforts and reducing biodiversity loss (Wu 2016). As a result, there is an immediate need to further increase funding for biodiversity data collection and capacity building, particularly in biodiversity-unique, data-poor Qinghai Province.

Acknowledgements

We are grateful to many colleagues at Institute of Geographic Sciences and Natural Resources, CAS, Forestry Department of Qinghai Province, and the State Forestry of Administration for their assistance in the data collection and processing. We especially thank Dr. Li Xinhai for the assistance in data collections. This study was funded by Forestry Science and Technology Demonstration Project (2017): Cobenefits between biodiversity conservation and carbon storage in Huangshui National Wetland Park, Program for developing unique institute of the Chinese Academy of Sciences (TSYJS05), The UNDP/GEF Qinghai Biodiversity Conservation Project, and the Natural Science Foundation of China (31400418).

References

Addison PFE, Rumpff L, Bau SS, Carey JM, Chee YE, Jarrad FC, Burgman MA (2013) Practical solutions for making models indispensable in conservation decision-making. Diversity and Distribution 19: 490–502. https://doi.org/10.1111/ddi.12054

Alroy J (2015) Current extinction rates of reptiles and amphibians. Proceedings of the National Academy of Sciences of the United States of America 112: 13003–13008. https://doi.org/10.1073/pnas.1508681112

Andrew ME, Wulder MA, Coops NC (2012) Identification of de facto protected areas in boreal Canada. Biological Conservation 146: 97–107. https://doi.org/10.1016/j.biocon.2011.11.029

Ball IR, Possingham HP, Watts M (2009) Marxan and relatives:software for spatial conservation prioritisationIn Spatial conservation prioritisation:quantitative methods and computational tools. Oxford University Press, Oxford, 185–195.

Carranza T, Balmford A, Kapos V, Manica A (2014) Protected area effectiveness in reducing conversion in a rapidly vanishing ecosystem: the Brazilian cerrado. Conservation Letters 7: 216–223. https://doi.org/10.1111/conl.12049

Carwardine J, Wilson KA, Ceballos G, Ehrlich PR, Naidoo R, Lwamura T, Possingham HP (2008) Cost effective priorities for global mammal conservation. Proceedings of the National Academy of Sciences of the United States of America 105: 11446–11450. https://doi.org/10.1073/pnas.0707157105

Carwardine J, Klein CJ, Wilson KA, Pressey RL, Possingham HP (2009) Hitting the target and missing the point:target-based conservation planning in context. Conservation Letters 2: 3–10. https://doi.org/10.1111/j.1755-263X.2008.00042.x

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM et al. (2000) Consequences of changing biodiversity. Nature 405: 239–242. https://doi.org/10.1038/35012241

Chen YH, Zhang J, Jiang JP, Nielsen SE, He FL (2017) Assessing the effectiveness of China's protected areas to conserve current and future amphibian diversity. Diversity and Distributions 23: 146–157. https://doi.org/10.1111/ddi.12508

Costa GC, Nogueira C, Machado RB, Colli GR (2010) Sampling bias and the use of ecological niche modeling in conservation planning: a field evaluation in a biodiversity hotspot. Biodiversity Conservation 19: 883–899. https://doi.org/10.1007/s10531-009-9746-8

Diminin E, Toivonen T (2015) Global protected area expansion: creating more than paper parks. Bioscience 65: 637–638. https://doi.org/10.1093/biosci/biv064

Fajardo J, Lessmann J, Bonaccorso E, Devenish C, Munoz J (2014) Combined use of systematic conservation planning, species distribution modelling, and connectivity analysis reveals severe conservation gaps in a Megadiverse Country (Peru) PLoS ONE 9: e114367. https://doi.org/10.1371/journal.pone.0114367

Franklin J (2013) Species distribution models in conservation biogeography:developments and challenges. Diversity and Distributions 19: 1217–1223. https://doi.org/10.1111/ddi.12125

Gaston KJ, Rodrigues ASL (2003) Reserve selection in regions with poor biological data. Conservation Biology 17: 188–195. https://doi.org/10.1046/j.1523-1739.2003.01268.x

Gray CL, Hill SLL, Newbold T, Hudson LN, Börger L et al. (2016) Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nature Communications 7: 12306. https://doi.org/10.1038/ncomms12306

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis L, Sutdiffe PR, Brotons L et al. (2013) Predicting species distributions for conservation decisions. Ecology Letters 16: 1424–1435. https://doi.org/10.1111/ele.12189

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H (2015) Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography 24: 276–292. https://doi.org/10.1111/geb.12268

Hermoso V, Kennard MJ (2012) Uncertainty in coarse conservation assessments hinders the efficient achievement of conservation goals. Biological Conservation 147(1): 52–59. https://doi.org/10.1016/j.biocon.2012.01.020

Hermoso V, Ward DP, Kennard MJ (2013) Prioritizing refugia for freshwater biodiversity conservation in highly seasonal ecosystems. Diversity and Distributions 19: 1031–1042. https://doi.org/10.1111/ddi.12082

Hernandez PA, Franke I, Herzog SK, Pacheco V, Paniagua L, Quintana HL, Soto A, Swenson JJ, Tovar C, Valqui TH, Vargas J, Young BE (2008) Predicting species distributions in poorly-studied landscapes. Biodiversity Conservation 17: 1353–1366. https://doi.org/10.1007/s10531-007-9314-z

Hijmans RJ, Cameron SEJ, Parra L, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. https://doi.org/10.1002/joc.1276

Huang YP (2013) Managing the Three-Rivers Headwater Region, China: From ecological engineering to social engineering. Ambio 42: 566–576. https://doi.org/10.1007/s13280-012-0366-2

Laurance WF, Useche DC, Rendeiro JR, Kalka M, Bradshaw C et al. (2012) Averting biodiversity collapse in tropical forest protected areas. Nature 489: 290–294. https://doi.org/10.1038/nature11318

Lawton JH, May RM (2005) Extinction Rates, Oxford University Press, Oxford.

Loiselle BA, Howell CA, Graham GH, Goerck JM, Brooks TM, Smith KG, Williams PH (2003) Avoiding pitfalls of using species distribution models in conservation planning. Conservation Biology 17: 1591–1600. https://doi.org/10.1111/j.1523-1739.2003.00233.x

Li RQ, Xu M, Wong MHG, Qiu S, Li XH, Ehrenfeld D, Li DM (2015) Climate change threatens giant panda protection in the 21st century. Biological Conservation 182: 93–101. https://doi.org/10.1016/j.biocon.2014.11.037

Li RQ, Tian HD, Li XH (2010) Climate change induced range shifts of Galliformes in China. Integrative Zoology 1: 153–162.

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28: 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Liu JG, Ouyang ZY, Pimm SL, Raven PH, Wang XK, Miao H, Han NY (2003) Protecting China's biodiversity. Science, 300: 1240–1241. https://doi.org/10.1126/science.1078868

Liu MC, Li DQ (2007) Study on biodiversity conservation priorities: Taking Sanjiangyuan Region. Journal of Natural Science of Hunan Normal University 30: 110–115. [In Chinese with English abstract]

Lombard AT, Cowling RM, Pressey RL, Rebelo AG (2003) Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. Biological Conservation 112: 45–62. https://doi.org/10.1016/S0006-3207(02)00422-6

Luo ZH, Jiang ZG, Tang SH (2015) Impacts of climate change on distributions and diversity of ungulates on the Tibetan Plateau. Ecological Applications 25: 24–38. https://doi.org/10.1890/13-1499.1

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405: 243–253. https://doi.org/10.1038/35012251

McPherson TY (2014) Landscape scale species distribution modeling across the Guiana Shield to inform conservation decision making in Guyana. Biodiversity Conservation 23: 1931–1948. https://doi.org/10.1007/s10531-014-0696-4

Ministry of Environmental Protection of the People's Republic of China (2011) The Strategy and Action Plan for Biodiversity Protection in China (2011–30), China Environmental Science Press, Beijing. [In Chinese with English abstract]

Pearson R, Raxworthy C, Nakamura M, Peterson A (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34: 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. Science 269: 347–350. https://doi.org/10.1126/science.269.5222.347

Polak T, Watson JEM, Fuller RA, Joseph LN, Martin TG, Possingham HP, Venter O, Carwardine J (2015) Efficient expansion of global protected areas requires simultaneous planning for species and ecosystems. Royal Society Open Science 2: 150107. https://doi.org/10.1098/rsos.150107

Ponce-Reyes R, Reynoso-Rosales VH, Watson JEM, VanDerWal J, Fuller RA, Pressey R, Possingham HP (2012) Vulnerability of cloud forest reserves in Mexico to climate change. Nature Climate Change 2: 448–452. https://doi.org/10.1038/nclimate1453

Powers RP, Coops NC, Nelson T, Wulder MA, Drever CR (2013) Integrating accessibility and intactness into large-area conservation planning in the Canadian boreal forest. Biological Conservation167: 371–379. https://doi.org/10.1016/j.biocon.2013.08.032

Powers RP, Coops NC, Tulloch VJ, Gergel SE, Nelson TA, Wulder MA (2016) A conservation assessment of canada's boreal forest incorporating alternate climate change scenarios. Remote Sensing in Ecology and Conservation. https://doi.org/10.1002/rse2.3

Proosdij ASJV, Sosef MSM, Wieringa JJ, Raes N (2015) Minimum required numbers of specimen records to develop accurate species distribution models. Ecography 39: 542–552. https://doi.org/10.1111/ecog.01509

Qu Y (2011) Conservation planning of biodiversity in the three rivers headwater Region in Qinghai Province. Thesis, Beijing Forestry University. [In Chinese with English abstract]

Rands MRW, Adams W, Bennun L, Butchart SHM, Clements A, Coomes D, Vira B (2010) Biodiversity Conservation: Challenges Beyond 2010. Science 329: 1298–1303. https://doi.org/10.1126/science.1189138

Rebelo H, Tarrosow P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16: 561–576. https://doi.org/10.1111/j.1365-2486.2009.02021.x

Rodrigues ASL, Akçakaya HR, Andelman SJ, Bakarr MI, Boitani L (2004) Global gap analysis: Priority regions for expanding the global protected-area network. Bioscience 54: 1092–1100. https://doi.org/10.1641/0006-3568(2004)054[1092:GGAPRF]2.0.CO;2

Rodrigues ASL, Akcakaya HR, Andelman SJ, Bakarr MI, Boitani L, Brooks TM et al. (2004) Global Gap Analysis: Priority regions for expanding the global protected-area network. Bioscience Reports 54: 1092–1100. https://doi.org/10.1641/0006-3568(2004)054[1092:GGAPRF]2.0.CO;2

Sanderson E, Segan DB, Watson JEM (2015) Global status of and prospects for protection of terrestrial geophysical diversity. Conservation Biology 29: 649–656. https://doi.org/10.1111/cobi.12502

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV (2002) The human footprint and the last of the wild. Bioscience 52: 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Tulloch VJD, Brown CJ, Possinghama HP, Jupiter SD, Maina JM (2016) Improving conservation outcomes for coral reefs affected by future oil palm development in Papua New Guinea. Biological Conservation 203: 43–54. https://doi.org/10.1016/j.biocon.2016.08.013

Venter O, Fuller RA, Segan DB, Carwardine J, Brooks T et al. (2014) Targeting global protected area expansion for imperiled biodiversity. PLoS Biology 12: e1001891. https://doi.org/10.1371/journal.pbio.1001891

Watson J, Fuller RA, Barr L (2008) Why are we still using a 'one size fits all' philosophy for systematic reserve planning in Australia. Conserv Biol 14: 233–235. https://doi.org/10.1071/PC080233

Watson J, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. Nature 515: 67–73. https://doi.org/10.1038/nature13947

Wu RD, Zhang S, Yu DW, Zhao P, Li XH et al. (2011) Effectiveness of china's nature reserves in representing ecological diversity. Frontiers in Ecology & the Environment 9: 383–389. https://doi.org/10.1890/100093

Wu RD, Long YC, Malanson GP, Garber PA, Zhang S, Li D, Duo H (2014) Optimized spatial priorities for biodiversity conservation in China: A systematic conservation planning perspective. PLoS ONE 9: e103783. https://doi.org/10.1371/journal.pone.0103783

Wu RD (2016) Conservation: big data boost in China. Nature 540(7631): 38–38. https://doi.org/10.1038/540038c

Xie Y, Chen Y, Zou XY, Wang D, Wang S (1997) Chinese Endangered Species Information System (CESIS). Biodiversity Science 5(4): 293–295. [In Chinese with English abstract]

Zhang LY, Luo ZH, Mallon D, Li CW, Jiang ZG (2016) Biodiversity conservation status in China's growing protected areas. Biological Conservation 210: 89–100. https://doi.org/10.1016/j.biocon.2016.05.005

Zhang L, Xu WH, Ouyang ZY, Zhu CQ (2014) Determination of priority nature CAs and human disturbances in the Yangtze River Basin, China. Journal of Nature Conservation 22: 326–336. https://doi.org/10.1016/j.jnc.2014.02.007

Nature Conservation 24: 21–41 (2018)
doi: 10.3897/natureconservation.24.21608
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Effectiveness of Natura 2000 system for habitat types protection: A case study from the Czech Republic

Vilém Pechanec[1], Ivo Machar[1], Tomáš Pohanka[1], Zdeněk Opršal[1], Frantisek Petrovič[2], Juraj Švajda[3], Lubomír Šálek[4], Karel Chobot[5], Jarmila Filippovová[1], Pavel Cudlín[6], Jitka Málková[1]

1 *Palacky University, Faculty of Science, 17 Listopadu 12, 771 46 Olomouc, Czech Republic* **2** *Constantine the Philosopher University, Faculty of Natural Science, A. Hlinku 1, 949 74 Nitra, Slovak Republic* **3** *Matej Bel University, Faculty of Science, Tajovského 40, 974 01 Banská Bystrica, Slovak Republic* **4** *Czech University of Life Sciences, Faculty of Forestry and Wood Sciences, Kamycka 129, 165 00 Prague, Czech Republic* **5** *Agency of Nature Conservation and Landscape Protection, Kaplanova 1931, Praha, Czech Republic* **6** *Global Change Research Institute, Academy of Science, Bělidla 986/4a, 603 00 Brno, Czech Republic*

Corresponding author: *Ivo Machar* (ivo.machar@upol.cz)

Academic editor: *C. Margules* | Received 16 October 2017 | Accepted 12 December 2017 | Published 4 January 2018

http://zoobank.org/A96D94B3-9474-486A-B9F9-D9953A353145

Citation: Pechanec V, Machar I, Pohanka T, Opršal Z, Petrovič F, Švajda J, Šálek L, Chobot K, Filippovová J, Cudlín P, Málková J (2018) Effectiveness of Natura 2000 system for habitat types protection: A case study from the Czech Republic. Nature Conservation 24: 21–41. https://doi.org/10.3897/natureconservation.24.21608

Abstract

In conservation biology, there is a general consensus that protected areas (PAs) are one of the most effective tools for biodiversity protection. Worldwide, the area of PAs is continually increasing. But is the effectiveness of biodiversity protection improving with it? Since many PAs only exist as “paper parks” (i.e. they exist on maps and in legislation but offer little actual protection), the answer is uncertain. Moreover, it has long been known that, not only an increase in the extent of PAs, but also the efficiency of their management is fundamentally important for effective nature conservation. Therefore, there is a wide-ranging discussion about the actual effectiveness of PAs and factors that influence it.

In the course of the EU pre-accession phase, a comprehensive field mapping of natural habitats took place in the Czech Republic in years 2001–2004. The mapping results were used to designate Special Areas of Conservation (SACs) as part of the Natura 2000 network.

In this study, the aim was to evaluate the effectiveness of this newly created system of SACs for protection of biodiversity represented by the mapped natural habitats. The NCEI index (Nature Conservation Effectiveness Index) was applied, calculated as the total area of a particular habitat type in all SACs in the Czech Republic divided by the total area of that same natural habitat in the entire Czech Republic. Habitat protection in the Czech Republic is focused primarily on the smallest types of rare habitats, many of which are classified as critically endangered. The Czech national system of SACs provides protection to a total of 4,491.68 km^2 of natural habitats. Based on these results, it can be concluded that the overall effectiveness of the SAC system in the Czech Republic, which is specifically aimed at protecting natural habitats, is low (NCEI = 0.36). Nevertheless, the critically endangered habitats receive maximum protection (NCEI = 1).

Keywords

Conservation effectiveness, natural habitats, mapping, Nature Conservation Effectiveness Index, Special Areas of Conservation

Introduction

The World Database on Protected Areas (WDPA), managed since 1981 by the UN Environment World Conservation Monitoring Centre based in Cambridge, UK, also included World Heritage sites such as the historic centre of Prague (Plesnik 2012). A significant shift in the international concept of PAs was brought in by a new definition proposed by IUCN in 2008 (Dudley et al. 2010). As claimed by the new definition, a protected area is a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values. According to Ervin et al. (2010), establishment of PAs and their community perception went through three distinct stages over the years: (1) A classic approach from the 19th century until the 1970s was based on the notion that PAs can exist independently from the surrounding landscape and the benefits of the PAs for the local population were considered irrelevant. (2) A modern approach, promoted with different intensity in different parts of the world, is based on a greater recognition of the needs of local residents in PAs. The cornerstone of the modern approach is the recognition of the fact that it is not enough for nature conservation to keep establishing new PAs as isolated islands of nature in the midst of a man-altered landscape, but that the actual effectiveness of the PAs is essential for maintaining biodiversity. (3) The current approach considers PAs as a strategy for sustaining life-giving processes in nature that provide benefits to society, anthropocentrically referred to as ecosystem services. Management of PAs is perceived as an interdisciplinary affair, beneficial to both nature and humans (Machar et al. 2016).

The extent of PAs worldwide is slowly but steadily increasing. More than 80% of today's PAs have been established after 1962, when the 1st World Congress on National Parks was held in Seattle (Chape et al. 2005). Between 1993 and 2008, the number of PAs in the world has doubled and their total area increased by 60% (UNEP 2008).

In 2010, the 10th COP to the CBD in Nagoya resulted in ambitious targets: to increase the area of the world PAs to 17% on land and 10% in the sea (including coastlines) by 2020, while ensuring that the applied conservation management is effective and the system of PAs is representative, interconnected and integrated into the surrounding unprotected landscape. In the context of ongoing climate changes, the importance of PAs for preserving biodiversity is further increasing and brings even more ambitious proposals. One of them suggests protecting a minimum of 25% of land and 15% of sea in order to maintain global priority areas for the conservation of global biodiversity and ecosystem services, particularly carbon sequestration (Conservation International 2010, Jenkins and Joppa 2009).

In the strongly anthropogenically altered Europe, nearly all PAs (90%) are smaller than 10 km^2 (Gaston et al. 2008), which makes it really difficult, for example, to effectively protect populations of large vertebrates (Kovarik et al. 2014).

Although the percentage limits for the total minimum extent of PAs on land and sea may be relatively good indicators of conservation effectiveness, it is obvious that these figures say nothing about whether the individual PAs are large enough, whether they are appropriately spatially arranged and whether they host key species and resources (Power et al. 1996). In other words, they say nothing about whether or not the PAs effectively fulfil their purpose (Hockings et al. 2006).

Worldwide, the area of PAs is continually increasing. But is the effectiveness of biodiversity protection improving with it? Since many PAs only exist as “paper parks” (i.e. they exist on maps and in legislation but offer little actual protection), the answer is uncertain. Moreover, it has long been known that not only an increase in the extent of PAs, but also the efficiency of their management is fundamentally important for effective nature conservation. Therefore, there is a wide-ranging discussion about the actual effectiveness of PAs and factors that influence them (Joppa and Pfaff 2009; Leverington et al. 2010; Simon et al. 2014).

In the post-World War II Czech Republic, the effectiveness of PAs has been addressed within the national framework of PAs with the aim of including all rare habitat types. This effort, however, had not been successful until the end of the 20th century (Bucek and Machar 2012). PAs, during the Communist era, were of a large extent but their conservation regime corresponded to that of “paper parks” (Lipsky 1995). These PAs received a real protection only after the change in the political regime in 1992 under the new Nature Conservation Act. In the course of the EU pre-accession phase, a comprehensive field mapping of natural habitats took place in the Czech Republic in the years 2001–2004. The mapping results were used to designate the Special Areas of Conservation (SACs) as a part of the Natura 2000 network.

The aim of this paper is to evaluate the effectiveness of the Natura 2000 network (Miko 2012), using the Czech Republic as a case study. To date, the effectiveness of PAs in the Natura 2000 network in protecting biodiversity has been addressed by a number of studies that generally confirm the positive protective effect of this European conservation concept. For example, Donald et al. (2007) showed that through establishing Special Protection Areas (SPAs), the Birds Directive successfully provides protection to the most endangered European bird species and it has prevented further decline of many bird populations. According to Sanderson et al. (2015), the bird species listed in Annex I of the Birds Directive show more positive trends both in short and long terms in comparison with species not listed in the Annex. The longer the enforcement of the Birds Directive in each particular country, the more obvious is the trend. Although protection of migratory birds on their nesting sites only, for example, is insufficient, it still has a demonstrable positive effect on these populations even in times of climate change. The SPAs also influence non-target species (Brodier et al. 2013). On the other hand, some SPAs in agricultural landscapes sustain target species and species adapted to fallow land but do not support other species (Santana et al. 2013). It is therefore necessary to also focus on non-target species and better link nature conservation and agricultural policy.

In this study, the effectiveness of the Natura 2000 network was analysed with a special focus on the SACs that are primarily designated to protect natural habitats. The aim of this paper was to evaluate the effectiveness of habitat conservation for all mapped natural habitats in the territory of the Czech Republic in the context of the Natura 2000 conservation objectives, i.e. preserving the existing character of the natural habitat types.

Materials and methods

To evaluate the effectiveness of SACs in the Czech Republic, data collected during a national habitat field survey conducted in the period 2001–2004 were used. The survey under the Habitats Directive, formally known as the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, was carried out over the entire territory of the Czech Republic on a scale of 1:10,000. The survey results were summarised in the Habitat Catalogue of the Czech Republic (hereinafter referred to as the "Catalogue") (Chytry et al. 2010) listing a total of 156 natural habitats (Table 1). The field survey provided detailed data on the diversity of canopy, shrub and herb layers of specific mapped habitat segments and basic data on ecological quality of individual habitats. All results have been completely digitised and used to designate Special Areas of Conservation as defined by Annex III of the Habitats Directive (Loncakova 2009).

Species rarity is usually evaluated based on three criteria: geographic distribution, habitat requirements and abundance. Species conservation efforts predominantly focus on habitat specialists with restricted distribution (e.g. endemic species or isolated relict populations of rare species) or species with a broad geographic range but strong ties to rare habitats. A similar approach is being applied to habitat protection. Particular attention is paid to unique habitats tied to geographically or ecologically rare phenomena (e.g. serpentinites or glacial corries). With more widespread habitats, conservation efforts focus on those that can only be found on very small areas with specific natural conditions (springs, salt marshes etc.). Therefore, data on abundance and distribution may provide sufficient guidance needed to assess the degree of vulnerability of individual habitat types. Following the publication of the Catalogue, the Red Book of Habitats of the Czech Republic (RBH) was produced in 2005 (Kučera 2012). Based on a detailed field survey, the Red Book of Habitats provides a critical evaluation of data on occurrence and spread of individual habitats

Table 1. Conservation effectiveness of natural habitats in the Czech Republic.

Habitat type	Natura 2000 habitat code	Habitat code (Chytrý et al. 2010)	Total area of habitat in Czech Republic [km^2]	Code of vulnerability (Kučera 2012)	Number of habitat segments in SAC	Total area of habitat in the SAC [km^2]	NCEI
Wind-swept alpine grasslands	6150	A1.1	1.65	VU	107	1.65	1
Closed alpine grasslands	6150	A1.2	7.59	VU	355	7.59	1
Alpine heathlands	4060	A2.1	1.26	VU	121	1.26	1
Subalpine *Vaccinium* vegetation	4060	A2.2	4.8	VU	455	4.8	1
Snow beds	6150	A3	0.02	CR	12	0.02	1
Subalpine tall grasslands	6430	A4.1	7.28	NT	821	7.28	1
Cliff vegetation in the Sudeten cirques	8220	A5	0.03	CR	11	0.03	1
Acidophilous vegetation of alpine cliffs	8220	A6B	0.41	NT	116	0.41	1
Pinus mugo scrub	4070	A7	12.17	VU	376	12.17	1
Salix lapponum subalpine scrub	4080	A8.1	0.04	CR	5	0.04	1
Subalpine deciduous tall scrub	4080	A8.2	0.29	NT	39	0.29	1
Low xeric scrub, secondary vegetation with *Prunus tenella*	40A0	K4B	0.01	CR	6	0.01	1
Calcareous fens with *Cladium mariscus*	7210	M1.8	0.04	CR	7	0.04	1
Vegetation of annual halophilous grasses	–	M2.4	0.04	CR	1	0.04	1
River gravel banks with *Myricaria germanica*	3230	M4.2	0.13	CR	1	0.13	1
River gravel banks with *Calamagrostis pseudophragmites*	3220	M4.3	0.07	EN	47	0.07	1
Subalpine springs	–	R1.5	0.07	VU	113	0.07	1
Peat soils with *Rhynchospora alba*	7150	R2.4	0.14	EN	48	0.14	1
Tall-forb vegetation of fine-soil-rich boulder screes	–	S1.4	0.06	VU	35	0.06	1
Subalpine *Nardus* grasslands	6230	T2.1	1.5	VU	296	1.5	1
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters with *Salvinia natans*	3150	V1D	0.05	EN	6	0.05	1
Isoëtes vegetation	3130	V6	0.25	CR	2	0.25	1
Acidophilous vegetation of alpine boulder screes	8110	A6A	1.84	NT	417	1.83	0.99
Montane *Nardus* grasslands with alpine species	6230	T2.2	7.86	VU	1293	7.8	0.99
Subalpine tall-fern vegetation	6430	A4.3	0.54	NT	123	0.53	0.98
Bog hollows	7110	R3.3	0.84	EN	253	0.81	0.96
Basiphilous vegetation of vernal therophytes and succulents with dominance of *Jovibarba globifera*	6110	T6.2A	1.11	EN	36	1.07	0.96
Pinus rotundata bog forests	91D0	L10.4	10.01	EN	119	9.54	0.95
Open raised bogs	7110	R3.1	6.31	EN	732	5.98	0.95
Raised bogs with *Pinus mugo*	91D0	R3.2	17.04	EN	616	16.11	0.95

Vegetation of exposed bottoms in warm areas	3130	M2.3	0.32	EN	8	0.29	0.91
Pannonian sand steppe grasslands	6260	T5.4	0.98	VU	62	0.89	0.91
Acidophilous thermophilous oak forests with *Genista pilosa*	91I0	L6.5A	2.17	VU	187	1.93	0.89
Narrow-leaved dry grasslands with significant occurrence of orchids	6210	T3.3C	0.35	VU	12	0.31	0.89
Broad-leaved dry grasslands with significant occurrence of orchids and without *Juniperus communis*	6210	T3.4C	9.74	VU	259	8.6	0.88
Peri-Alpidic serpentine pine forests	–	L8.3	0.45	EN	33	0.39	0.87
Pannonian thermophilous oak forests on loess	91I0	L6.2	16.54	VU	371	13.98	0.85
Degraded raised bogs	7120	R3.4	7.85	NT	377	6.65	0.85
Montane sycamore-beech forests	9140	L5.2	9.21	VU	686	7.73	0.84
Montane *Calamagrostis* spruce forests	9410	L9.1	438.81	VU	6485	366.79	0.84
Montane grey alder galleries	91E0.	L2.1	5.56	VU	671	4.64	0.83
Calcareous fens	7230	R2.1	0.4	VU	77	0.33	0.83
Boreo-continental pine forests with lichens on sand	91T0	L8.1A	11.73	VU	718	9.53	0.81
Willow scrub of river gravel banks	3240	K2.2	0.76	VU	153	0.61	0.8
Sesleria grasslands	6190	T3.2	0.38	VU	144	0.3	0.79
Dry lowland and colline heaths with occurrence of *Juniperus communis*	5130	T8.1A	0.14	VU	26	0.11	0.79
Montane *Athyrium* spruce forests	9410	L9.3	9.44	EN	355	7.25	0.77
Peri-Alpidic basiphilous thermophilous oak forests	91H0	L6.1	9.11	VU	468	6.91	0.76
Sub-Pannonian steppic grasslands	6240	T3.3A	3.46	VU	293	2.62	0.76
Unvegetated river gravel banks	–	M4.1	1.82	VU	438	1.37	0.75
Pannonian loess steppic grasslands	6250	T3.3B	0.76	EN	46	0.57	0.75
Continental inundated meadows	6440	T1.7	11.56	EN	319	8.49	0.73
Bog spruce forests	91D0	L9.2A	60.02	EN	1935	43.05	0.72
Continental tall-forb vegetation	6430	T1.8	0.07	CR	6	0.05	0.71
Hardwood forests of lowland rivers	91F0	L2.3	241.38	EN/VU	6140	170.07	0.7
Transitional mires	7140	R2.3	29.81	EN	2971	20.97	0.7
Macrophyte vegetation of water streams with currently present aquatic macrophytes	3260	V4A	29.71	NT	738	20.73	0.7
Pannonian thermophilous oak forests on sand	91I0	L6.3	13.73	VU	384	9.54	0.69
Submontane and montane *Nardus* grasslands with scattered *Juniperus communis* vegetation	5130	T2.3A	3.32	VU	461	2.27	0.68
Ribes alpinum scrub on cliffs and boulder screes	–	S1.5	0.36	VU	193	0.24	0.67
Mobile screes of basic rocks	8160	S2A	0.24	VU	67	0.16	0.67
Subalpine tall-forb vegetation	6430	A4.2	0.41	NT	169	0.27	0.66
Broad-leaved dry grasslands with significant occurrence of orchids and with *Juniperus communis*	6210	T3.4A	0.6	EN	21	0.39	0.65

Pannonian-Carpathian oak-hornbeam forests	91G0	L3.3A	42.59	---	794	27.12	0.64
Limestone beech forests	9150	L5.3	9.6	VU	362	6.19	0.64
Annual vegetation on wet sand	3130	M2.2	0.11	VU	14	0.07	0.64
Acidic moss-rich fens	7140	R2.2	20.83	VU	1887	13.08	0.63
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters with *Hydrocharis morsusranae*	3150	V1A	0.13	VU	59	0.08	0.62
Basiphilous vegetation of vernal therophytes and succulents without dominance of *Jovibarba globifera*	6110	T6.2B	0.41	VU	129	0.25	0.61
Waterlogged spruce forests	9410	L9.2B	298.13	VU	6799	178.49	0.6
Pannonian oak-hornbeam forests	91G0	L3.4	57.05	VU	1284	33.6	0.59
Secondary submontane and montane heaths with occurrence of *Juniperus communis*	5130	T8.2A	0.63	VU	60	0.37	0.59
Macrophyte vegetation of shallow still waters with dominant *Hottonia palustris*	–	V2B	0.29	EN	128	0.17	0.59
Birch mire forests	91D0	L10.1	14.48	EN	469	8.23	0.57
Rock-outcrop vegetation with *Festuca pallens*	6190	T3.1	3.15	NT	603	1.77	0.56
Broad-leaved dry grasslands without significant occurrence of orchids and with *Juniperus communis*	5310	T3.4B	1.25	VU	56	0.69	0.55
Vaccinium vegetation of cliffs and boulder screes	4030	T8.3	3.12	VU	689	1.68	0.54
Forest springs with tufa formation	7220	R1.3	0.19	VU	264	0.1	0.53
Broad-leaved dry grasslands without significant occurrence of orchids and without *Juniperus communis*	6210	T3.4D	110.76	NT	3476	57.76	0.52
Low xeric scrub, primary vegetation on rock outcrops with *Cotoneaster* spp.	40A0	K4A	0.7	VU	220	0.36	0.51
Pine forests of continental mires with *Eriophorum*	91D0	L10.3	0.73	EN	20	0.37	0.51
Chasmophytic vegetation of calcareous cliffs and boulder screes	8210	S1.1	1.85	VU	533	0.95	0.51
Dry herbaceous fringes	–	T4.1	2.04	NT	381	1.03	0.5
Herb-rich beech forests	9130	L5.1	1229.3	LC	20798	607.61	0.49
Acidophilous beech forests	9110	L5.4	1473.99	LC	24203	726.52	0.49
Riverine reed vegetation	–	M1.4	12.88	VU	1665	6.17	0.48
Submontane and montane *Nardus* grasslands without *Juniperus communis*	6230	T2.3B	88.12	NT	5285	42.64	0.48
Narrow-leaved dry grasslands without significant occurrence of orchids	6210	T3.3D	16.13	VU	766	7.65	0.47
Macrophyte vegetation of oligotrophic lakes and pools	3160	V3	0.3	EN	88	0.14	0.47
Forest-steppe pine forests	91U0	L8.2	3.84	VU	110	1.76	0.46
Acidophilous dry grasslands with significant occurrence of orchids	6210	T3.5A	0.26	VU	12	0.12	0.46

Secondary submontane and montane heaths without occurrence of *Juniperus communis*	4030	T8.2B	12.47	NT	749	5.69	0.46
Muddy river banks	3270	M6	0.66	NT	103	0.29	0.44
Montane *Trisetum* meadows	6520	T1.2	160.31	NT	4979	70.52	0.44
Acidophilous vegetation of vernal therophytes and succulents without dominance of *Jovibarba globifera*	8230	T6.1B	1.3	VU	266	0.57	0.44
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters with *Stratiotes aloides*	3150	V1B	0.09	EN	10	0.04	0.44
Chasmophytic vegetation of siliceous cliffs and boulder screes	8220	S1.2	54.92	NT	7946	23.49	0.43
Mobile screes of acidic rocks	8150	S2B	0.83	VU	107	0.35	0.42
Macrophyte vegetation of water streams with potential occurrence of aquatic macrophytes or with natural or semi-natural bed	3260	V4B	66.56	LC	1719	27.94	0.42
Petasites fringes of montane brooks	6430	M5	3.67	VU	787	1.46	0.4
Willow-poplar forests of lowland rivers	91E0.	L2.4	26.5	VU	1134	10.41	0.39
Central European basiphilous thermophilous oak forests	91I0	L6.4	39.18	NT	677	15.38	0.39
Low xeric scrub, other stands	–	K4C	0.21	VU	97	0.08	0.38
Vegetation of perennial amphibious herbs	3130	M3	0.32	NT	44	0.12	0.38
Acidophilous thermophilous oak forests without *Genista pilosa*	91I0	L6.5B	66.13	NT	1441	24.66	0.37
Alder carrs	–	L1	37.47	VU	1171	13.44	0.36
Intermittently wet *Molinia* meadows	6410	T1.9	84.15	VU	2500	30.15	0.36
Dry lowland and colline heaths without occurrence of *Juniperus communis*	4030	T8.1B	1.79	VU	246	0.64	0.36
Forest springs without tufa formation	–	R1.4	8.6	NT	4078	3.02	0.35
Pine mire forests with *Vaccinium*	91D0	L10.2	43.73	VU	419	15.04	0.34
West Carpathian oak-hornbeam forests	9170	L3.3B	394.98	---	4913	134.5	0.34
Ravine forests	9180	L4	209.34	VU	5237	71.5	0.34
Herbaceous fringes of lowland rivers	6430	M7	1.46	NT	99	0.49	0.34
Meadow springs with tufa formation	7220	R1.1	0.12	VU	76	0.04	0.33
Caves not open to the public	8310	S3B	0.03	NT	106	0.01	0.33
Charophyceae vegetation	3140	V5	0.3	NT	60	0.1	0.33
Willow carrs	–	K1	59.64	VU	3849	18.8	0.32
Halophilous reed and sedge beds	–	M1.2	0.89	EN	31	0.27	0.3
Subcontinental pine-oak forests	–	L7.3	259.27	NT	3201	76.46	0.29
Tall-sedge beds	–	M1.7	76.81	VU	3788	22.55	0.29
Meadow springs without tufa formation	–	R1.2	0.89	VU	360	0.26	0.29

Acidophilous vegetation of vernal therophytes and succulents with dominance of *Jovibarba globifera*	8230	T6.1A	0.07	VU	16	0.02	0.29
Mesotrophic vegetation of muddy substrata	7140	M1.6	0.64	EN	74	0.18	0.28
Alluvial *Alopecurus* meadows	–	T1.4	159.57	VU	1628	44.04	0.28
Open sand grasslands with *Corynephorus canescens*	2330	T5.2	1.56	EN	81	0.44	0.28
Tall mesic and xeric scrub	–	K3	351.9	LC	12146	92.46	0.26
Hercynian oak-hornbeam forests	9170	L3.1	1010.61	NT	11806	263.77	0.26
Tall grasslands on rock ledges	–	S1.3	1.1	VU	165	0.29	0.26
Acidophilous dry grasslands without significant occurrence of orchids	6210	T3.5B	17.43	NT	595	4.59	0.26
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters without species specific to V1A–V1E	3150	V1F	70.05	VU	1316	18.54	0.26
Macrophyte vegetation of shallow still waters, other stands	–	V2C	1.6	NT	189	0.41	0.26
Reed beds of eutrophic still waters	–	M1.1	102.05	NT	3108	25.73	0.25
Wet *Filipendula* grasslands	6430	T1.6	129.65	LC	4736	32.4	0.25
Willow scrub of loamy and sandy river banks	–	K2.1	35.93	NT	1691	8.64	0.24
Mesic herbaceous fringes	–	T4.2	9.79	VU	916	2.37	0.24
Inland salt marshes	1340	T7	1.18	EN	34	0.28	0.24
Wet *Cirsium* meadows	–	T1.5	416.78	NT	11645	90.46	0.22
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters without macrophyte species valuable for nature conservation	–	V1G	203.02	VU	1577	44.44	0.22
Macrophyte vegetation of shallow still waters with dominant *Batrachium* spp.	–	V2A	1.74	NT	49	0.39	0.22
Boreo-continental pine forests, other stands	–	L8.1B	135.64	NT	2173	28.45	0.21
Vegetation of exposed fishpond bottoms	3130	M2.1	7.79	VU	233	1.66	0.21
Mesic *Arrhenatherum* meadows	6510	T1.1	1907.16	LC	22692	407.23	0.21
Vegetation of wet disturbed soils	–	T1.10	6.68	NT	1044	1.38	0.21
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters with *Utricularia australis* or *U. vulgaris*	3150	V1C	3.1	VU	133	0.65	0.21
Eutrophic vegetation of muddy substrata	–	M1.3	3.75	VU	473	0.74	0.2
Cynosurus pastures	–	T1.3	408.56	NT	3920	81.16	0.2
Ash-alder alluvial forests	91E0.	L2.2	796.06	VU/LC	13814	149.47	0.19
Reed vegetation of brooks	–	M1.5	3.97	VU	505	0.7	0.18
Wet acidophilous oak forests	9190	L7.2	104.14	VU	842	18.15	0.17
Polonian oak-hornbeam forests	9170	L3.2	112.58	VU	864	17.69	0.16
Annual vegetation on sandy soils	2330	T5.1	0.55	EN	31	0.09	0.16
Dry acidophilous oak forests	–	L7.1	397.53	NT	2967	59.03	0.15

Acidophilous grasslands on shallow soils	–	T5.5	15.57	NT	397	1.8	0.12
Festucas and grasslands	2330	T5.3	6.75	VU	151	0.67	0.1
Acidophilous oak forests on sand	–	L7.4	10.86	NT	21	0.52	0.05
Caves open to the public	–	S3A	0.01	NT	23	0	0
Macrophyte vegetation of naturally eutrophic and mesotrophic still waters with *Aldrovanda vesiculosa*	3150	V1E	0.03	CR	0	0	0
Total of natural habitats	**–**	**---**	**12445.49**		**255244**	**4491.68**	**0.36**
Forest clearings	–	X10	318.01	---	9976	150.9	0.47
Stands of early successional woody species valuable for nature conservation	–	X12A	167.19	---	6778	79.29	0.47
Forest plantations of allochtonous coniferous trees	–	X9A	4867.39	---	47318	2022.37	0.42
Anthropogenic areas with sparse vegetation outside human settlements	–	X6	52.85	---	3198	20.52	0.39
Other stands of early successional woody species	–	X12B	103.83	---	5996	39.54	0.38
Herbaceous ruderal vegetation outside human settlements, stands valuable for nature conservation	–	X7A	81.02	---	2338	30.29	0.37
Forest clearings	–	X11	244.3	---	7476	86.79	0.36
Streams and water-bodies without vegetation valuable for nature conservation	–	X14	125.3	---	1452	43.25	0.35
Herbaceous ruderal vegetation outside human settlements, other stands	–	X7B	115.38	---	4718	39.36	0.34
Forest plantations of allochtonous deciduous trees	–	X9B	184.04	---	4197	61.05	0.33
Urbanised areas	–	X1	537.07	---	12675	173.41	0.32
Intensively managed meadows	–	X5	1212.39	---	8924	361.09	0.3
Stands of early successional woody species	–	X12	203.76	---	9585	59.69	0.29
Extensively managed fields	–	X3	104.72	---	1947	30.09	0.29
Scrub with ruderal or alien species	–	X8	14.3	---	774	4.2	0.29
Intensively managed fields	–	X2	738.66	---	1336	208.85	0.28
Woody vegetation outside forest and human settlements	–	X13	124.66	---	5405	32.84	0.26
Herbaceous ruderal vegetation outside human settlements	–	X7	159.3	---	5592	39.78	0.25
Permanent agricultural crops	–	X4	19.19	---	103	3.67	0.19
Total of non-natural habitats	**–**	**–**	**9373.36**		**139788**	**3486.98**	**0.37**

in the Czech Republic and defines the current status of habitats in terms of their threats, rarity and level of protection at the national scale. The categories of habitat vulnerability for specific habitats according to the RBH are listed in Table 1. The RBH is therefore being used as a professional basis for conservation of rare habitat types by means of PAs.

The NCEI index (Nature Conservation Effectiveness Index) was applied to measure the effectiveness of habitat conservation. The NCEI is calculated for specific habitat types as the total area of a particular habitat type in all SACs in the Czech Republic ($TANH_{SAC}$) divided by the total area of that same natural habitat in the entire Czech Republic ($TANH_{cz}$):

$$NCEI = TANH_{SAC} / TANH_{cz}$$

The NCEI index ranges from 0 (absence of protection) to 1 (totally effective protection). The calculated value of NCEI > 0.75 indicates a highly effective habitat protection (more than 75% of the total area of all identified natural habitats are protected by means of SACs), values between 0.74–0.50 indicate intermediate habitat protection (more than 50% of the total area of natural habitats are integrated in SACs) and values NCEI ≤ 0.49 indicate low habitat protection (SACs cover less than 50% of the total area of a particular natural habitat). To determine the NCEI index, two GIS datasets, administered by the Nature Conservation Agency of the Czech Republic, were used: 1) the habitat mapping layer and 2) the SAC border layer. All data (in vector format – *Esri geodatabase* and national coordinate system – epsg: 5514) were processed in ArcGIS 10.4. GIS technologies represent a very effective tool for deriving both primary and entirely new values that are applicable in the decision support process (Pechanec et al. 2015).

First, the total area of individual habitats in the entire Czech Republic was determined.

As the GIS layer of mapped habitats included habitat mosaics (i.e. areas for which one GIS feature is associated with several habitat types recorded in one data row), these mosaics had to be broken down into individual parts using a string of functions in Python language: a mosaic broken down into 2–6 items (i.e. separate attribute columns) was iteratively scanned using the *Select by Attributes* function in order to identify individual habitat codes. After identifying all habitat codes, the proportion of each habitat using the *Field Calculator* tool was determined. The unique values used for the identification were the habitat codes as listed in the Catalogue. To summarise the selected segments and calculate their areas, the *Summarise* and *Calculate Geometry* functions, respectively, were used. In the second phase, the habitat types in individual SACs were determined. The SAC border layer was then used to clip the national layer of habitats using the *Clip* function. The process of identifying, summarising and updating the selection was then repeated for the segments located within the SACs. Using the *Field Calculator*, the NCEI index was calculated and these figures were exported to the resulting table (Table 1).

Results

Natural habitats (156 types) cover 15.8% of the area of the Czech Republic (Table 1). The total of 255,244 mapped natural habitat segments occupies 12,445.49 km^2.

There are 55 (mostly non-forest) habitat types in the Czech Republic with a total area smaller than 1 km^2 (Table 1). Of these small-scale habitat types, 17 cover less than 0.10 km^2. The rarest habitats in the Czech Republic (based on their total area and a total number of mapped segments) are Snow beds (A3), Cliff vegetation in the Sudeten cirques (A5) and

Salix lapponum subalpine scrub (A8.1), all critically endangered due to climate-induced changes in vegetation zones in the Czech Republic (Machar et al. 2017a). Critically endangered are also Low xeric scrubs with *Prunus tenella* (K4B) with six mapped segments, Calcareous fens with *Cladium mariscus* (M1.8) with seven segments and two habitat types found at a single locality in the Czech Republic – Vegetation of annual halophilous grasses (M2.4) and River gravel banks with *Myricaria germanica* (M4.2) of the Bečva River. Only two sites are known for the unique aquatic habitat of Oligotrophic standing waters with *Isoëtes* vegetation (V6) in the Sumava National Park. Both Continental tall-forb vegetation (T1.8) and Still waters with *Salvinia natans* (V1D) have been found in six mapped segments. Very rare habitats with only a few known localities in the Czech Republic are T6.1A, V1B and V1E (Tab. 1). A very small area of the Czech Republic is occupied by Subalpine springs (R1.5, 0.07 km^2) and Tall-forb vegetation of fine-soil-rich boulder screes (S1.4, 0.06 km^2). The group of small-scale natural habitats also includes two unique habitat types with a very small total area: Caves open to the public (S3A), which receive sufficient protection through a strict visitor regime limiting both the number and frequency of visits (Hromas 2009) and Caves not open to the public (S3B; 106 localities), for which only entrance cave portals, typically not larger than few square metres, were mapped as natural habitats.

Habitat protection in the Czech Republic is concentrated primarily on these smallest types of rare habitats. The maximum protection (NCEI = 1) in the form of PAs applies to 22 types of natural habitats (Fig. 1). The maximum protection is given, for example, to 1) almost all natural habitats of the alpine zone above the tree line, which represent a unique environment threatened by the climate-induced upward tree-line shift (Machar et al. 2017b; Šenfeldr and Maděra 2011) and 2) River gravel banks with *Calamagrostis pseudophragmites* (M4.3), a rare habitat threatened by river regulations (Kilianova et al. 2017).

The highly effective habitat protection (NCEI = 0.99-0.75) is provided to 19 non-forest habitat types (Fig. 1), including rare alpine habitats, various types of peat bogs and small-scale segments of thermophilous lawns from the Pannonian biogeographical region, which extends to the southern part of the Czech Republic and by 10 rare forest habitat types from all forest vegetation zones present in the Czech Republic, representing unique examples of potential natural vegetation of the temperate forest of the European temperate zone.

Thirty-two natural habitats are associated with the intermediate effectiveness of habitat protection (NCEI = 0.74-0.50) (Fig. 1). This group of natural habitats includes those from the EN and VU categories of the threat classification list (Tab. 1), with the exception of two azonal forest types with a larger total area – L2.3. Hardwood floodplain forests of lowland rivers (TANHcz = 241 km^2, NCEI = 0.70) and L9.2B Waterlogged spruce forests (TANHcz = 298 km^2, NCEI = 0.60) are all of a small extent.

The majority (n = 73, Fig. 1) of natural habitat types in the Czech Republic is associated with low effectiveness of habitat protection (NCEI ≤ 0.49). Five habitat types from this group (four forest habitats L2.2, L3.1, L5.1, L5.4 and one non-forest habitat T1.1) have a total area of more than 500 km^2. The low protection effectiveness of these natural habitats reflects their large total area within the Czech Republic and the fact that the maintenance of their character (as defined in the Catalogue) is directly affected by

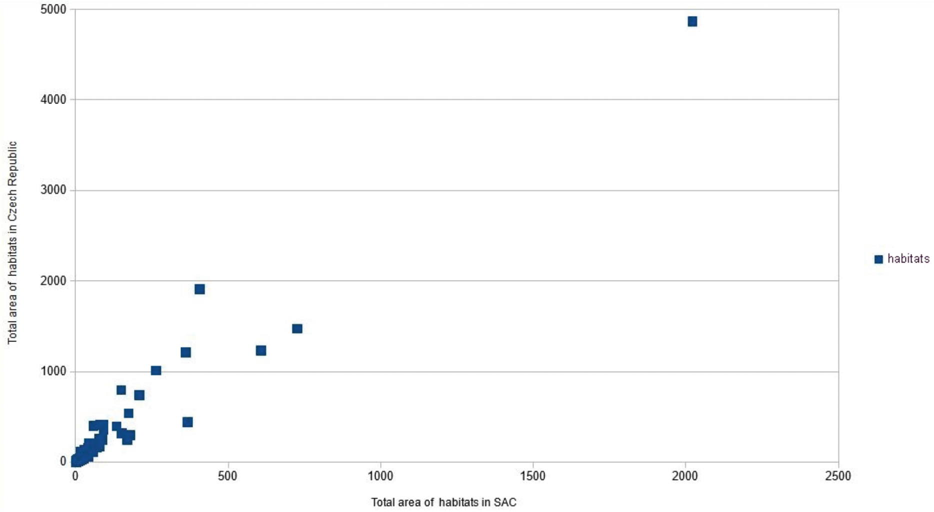

Figure 1. Area of natural habitats in the Czech Republic.

specific anthropogenic activities for which the SAC protection regime is not required. For instance, in order to maintain the defined character of L2.2 Ash-alder alluvial forests (TANHcz = 796 km^2, NCEI = 0.19), it is necessary to prevent eutrophication of the herb layer by nutrients supply from the surrounding (usually agricultural) land. For this particular habitat, changing the agricultural nitrogen management on the surrounding land is therefore of higher importance than declaring the SAC. Maintaining the defined character of L3.1 Hercynian oak-hornbeam forests (TANH$_{cz}$ = 1,010 km^2, NCEI = 0.26) requires re-implementation of the now defunct forest management type – coppice and coppice-with-standards (Machar 2009; Maděra et al. 2017). Functioning of the natural dynamics of beech forest habitats (L5.1 Herb-rich beech forests, TANH$_{cz}$ = 1,229 km^2, NCEI = 0.49 and L5.4 Acidophilous beech forests TANH$_{cz}$ = 1,473 km^2, NCEI = 0.49) depends on the natural beech restoration which is, however, being prevented by the overpopulation of deer (Machar et al. 2017c) due to the absence of their natural predators (Kovarik et al. 2014). The T1.1 Mesic Arrhenatherum meadows (TANH$_{cz}$ = 1,907 km^2, NCEI = 0.21) habitat is existentially dependent on regular mowing.

The Czech national system of SACs protects a total of 4,491.68 km^2 of natural habitats. Based on the NCEI value of 0.36, it can be concluded that the overall effectiveness of the SAC system in the Czech Republic (specifically aimed at protecting natural habitats) is low (Table 1). Nevertheless, the critically endangered habitats receive the maximum protection (NCEI = 1)

Discussion and conclusion

A large part of the territory of the Czech Republic, similarly to other Central European countries, is covered by human-altered land (Romportl et al. 2013), which does not meet the definition of natural habitats as described in the Catalogue. The controversial topic on "what are the conservation priorities – conservation of species or natural processes?" is being widely discussed in the Central European cultural landscape (Oprsal et al. 2016). Protection of natural habitats by creating PAs with non-intervention management or appropriate adaptive management may be one of the possible compromise solutions to this dilemma for nature conservation of Central European (Skokanova and Eremiasova 2013).

To maintain a stable habitat character as defined by the Catalogue, the majority of the habitat types in the Czech Republic require various levels of anthropogenic interventions or extensive farming, respecting the principles of ecosystem management (Grumbine 1994). Generally, it is impossible to define what type of habitat most influenced this result and if it is really low or not. Thus the authors' own expert range of NCEI (see above in section Methods) has been applied. In order to maintain the diversity of these natural habitats, conservation priorities will therefore need to be sought in methods of ecologically sound management rather than in further expansion of PAs. A study by Hoekstra et al. (2005) brought significant findings for defining global conservation priorities for the establishment of PAs. The study was based on an analysis of individual world biomes and their Conservation Risk Index (CRI; similar to the NCEI index used in this study). Contrary to the traditional belief about a need for priority conservation of the tropical rainforest, the study has shown that the grasslands and Mediterranean communities (biomes) are significantly more endangered. And the fact that the world's most endangered biomes are protected even less than the tundra and taiga biomes, which are least affected by humans, can be described as a global failure of nature conservation. A more recent study by Coad et al. (2009) newly reports that for 11 out of 14 biomes, the goal of protecting 10% of their area has been reached. Nevertheless, the terrestrial PAs rarely adequately encompass inland water ecosystems which are often not even listed amongst biomes (Herbert et al. 2010).

The habitat threat classification list used in this paper (Table 1) is based on the Czech national Red Book of Habitats (Divisek et al. 2014). The red list categories usually stem from the IUCN databases. The used criteria, however, are formulated for species and their population characteristics with respect to the degree of their isolation from other populations and are therefore difficult to apply to habitats. While for species which can be mapped e.g. local or endemic populations, a combined influence of a particular site and a vegetation type have to be taken into account for habitats. For this reason, the general criteria are applied in a process proposed by Gardenfors et al. (2001). According to this study, the global risk criteria can be only applied to habitats on a regional scale provided those are geographically isolated and without a continuous distribution across Europe.

The WDPA is currently a comprehensive global inventory of the world's PAs that 1) comply with the above mentioned IUCN definition from 2008, 2) for which exact spatial data (and designated boundaries) are known, 3) that have an assigned protected area category based on relevant national legislation, 4) for which year of designation or establishment is known and 5) all the data sources are appropriately quoted. As not all PAs meet these requirements, it is clear that even this most reputable database on PAs does not encompass all PAs worldwide (Rodrigues et al. 2004a). According to Visconti et al. (2013), only those areas which are listed in the WDPA, have a clearly defined management and therefore a clearly assigned IUCN category should be considered PAs. In this paper, the concept of SACs, corresponding with the IUCN categories 1–4, is followed.

It was not possible to focus on all of PAs categories in the Czech Republic (there are: national parks, protected landscape areas (PLAs), nature reserves, nature monuments, see in detail Machar 2012). Many of these categories of PLAs in the Czech Republic are overlapping each other (e.g. many of small nature reserves and nature monuments are situated in the area of large protected landscape areas or national parks). This fact comes from the long-term history of the system of PAs in the territory of the Czech Republic, which has resulted in current complicated overlapping layers of different types/categories of PLAs. Thus it is not possible to assess NCEI precisely for current situation of PLAs.

It is generally evident that the data on the total number and extent of PAs do not adequately reflect the effectiveness of the global system of PAs in protecting biodiversity (Rodrigues et al. 2004b). Nevertheless, a number of studies investigating the effectiveness of PAs based on analyses of their extent have provided crucial information for defining conservation priorities. A pioneering study by Prendergast et al. (1993) has surprisingly shown that the territorial overlap of occurrence of various species is very small and therefore not directly applicable for designing protected area networks. A comprehensive analysis of bird distribution by Orme et al. (2005) has shown that territorial overlaps of biodiversity hotspots and sites with endemic and endangered species are almost non-existent. According to Turner et al. (2007), the overlap of priority areas for biodiversity conservation and areas providing important ecosystem services varies greatly in different parts of the world (and is the largest in tropical rainforests due to high primary productivity). This is quite understandable, as PAs have been established for purposes other than the maintenance of ecosystem services. Not even exceptionally large PAs represent an optimum solution (Mittermeier et al. 2003; Olson and Dinerstein 2002), even though they usually encompass wilderness little affected by humans and more resistant to disruptive anthropogenic influences than PAs of a small extent (Cantú-Salazar and Gaston 2010). Similarly, regional studies of the Natura 2000 network show that territorial overlaps of sites with significant biodiversity (e.g. regional hotspots) and PAs are minor and the entire network may not be very effective (Dimitrakopoulos et al. 2004; Jantke et al. 2011; Wesolowski 2005).

Alongside the process of searching answers to the questions "how much and what kind of biodiversity is actually comprised in PAs?" or "are PAs managed to fulfil their role in protecting biodiversity and maintaining ecosystem services?" a new field has emerged, called conservation planning (Margules and Sarkar 2007). Despite a considerable development of this field, however, there is yet no generally accepted approach to evaluation of the effectiveness of PAs management. Meanwhile, the conceptual procedure proposed by the IUCN (Alexander 2008) is being used most often. According to the IUCN approach, good conservation management is based on an understanding of the existing values and threats of the protected area, followed by rational planning and fundraising. Moreover, it should foster ecosystem services that provide specific benefits to local people. This conceptual approach has been developed into several methodological tools, such as RAPPAM (Ervin 2003) or METT (Stoll-Kleemann 2010). Using this approach, IUCN has carried out the most extensive global assessment of the effectiveness of PAs. The assessment has revealed that only about 20% of evaluated sites provide an adequate level of nature protection and 14% of sites have serious deficiencies, with a lack of finances identified as a major problem (McDonald and Boucher 2011). Further, the analysis confirmed that local residents receive a significant income based on the existence of those PAs in which administrators inform in a timely and objective manner about prepared management plans and involve the residents in the implementation process.

When trying to assess the effectiveness of PAs, some studies have focused on determining the species richness of wild plants and animals living in the PAs. For this purpose, gap analyses have been used at different scales – for example Tantipisanuh et al. (2016). According to gap analyses by Ricketts et al. (2005), 764 endangered species of mammals, birds, amphibians and conifers occur only in a single protected site.

The study presented from the Czech Republic should be considered as a special type of gap analyses based on detailed habitat mapping. As was indicated, natural habitat protection in the Czech Republic is focused primarily on the smallest types of rare habitats, many of which are classified as critically endangered. The Czech national system of SACs provides protection to a total of 4,491.68 km^2 of natural habitats. Based on the presented results, it can be concluded that the overall effectiveness of the SAC system (a part of Natura 2000 network) in the Czech Republic, which is specifically aimed at protecting natural habitats, is low (NCEI = 0.36). Nevertheless, the critically endangered habitats receive a maximum protection (NCEI = 1). Methods used in this study can be applied in other European countries which have similar datasets from habitat mapping under Natura 2000 network establishment. Comparison of Natura 2000 network effectiveness both at national and European scale seems to be an important future conservation research challenge.

Acknowledgements

This study was supported by the Ministry of Education, Youth and Sports of the Czech Republic within the National Sustainability Program I (NPU I), grant number LO1415.

References

Alexander M (2008) Management Planning for Nature Conservation. Springer, Berlin, 1–425.

Brodier S, Augiron S, Cornulier T, Bretagnolle V (2013) Local improvement of skylark and corn bunting population trends on intensive arable landscape: a case study of the conservation tool Natura 2000. Animal Conservation 17: https://doi.org/10.1111/acv.12077

Bucek A, Machar I (2012) Application of Landscape Ecology in the Assessment of Anthropogenic Impacts of the Landscape. Palacky University, Olomouc, 1–153. [Accession Number: WOS 000331016000003]

Cantú-Salazar L, Gaston KJ (2010) Very Large Protected Areas and Their Contribution to Terrestrial Biological Conservation. BioScience 60(10). https://doi.org/10.1525/bio.2010.60.10.7

Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society B, Biological Sciences 360. https://doi.org/10.1098/rstb.2004.1592

Chytry M, Kucera T, Koci M, Grulich V, Lustyk P (2010) Habitat Catalogue of the Czech Republic. Agency of Nature Conservation and Landscape Protection,Prague, 1–445.

Coad L, Burgess ND, Loucks C, Fish L, Schlaremann JPW, Duarte L, Besancon B (2009) The ecological representativeness of the global protected areas estate in 2009: Progress towards the CBD target. UNEP-WCMC, Cambridge, 1–132.

Conservation International (2010) A rationale for protecting at least 25 % of Earth´s land and 15 % of Earth´s oceans to protect global biodiversity and ecosystem services. Technical Brief of Conservation International, Aarlington, 1–26.

Dimitrakopoulos PG, Memtsas D, Troumbis AY (2004) Questioning the effectiveness of the Natura 2000 Special Areas of Conservation strategy: the case of Crete. Global Ecology and Biogeography 13(3). https://doi.org/10.1111/j.1466-822X.2004.00086.x

Divisek J, Chytry M, Grulich V, Polakova L (2014) Landscape classification of the Czech Republic based on the distribution of natural habitats. Preslia 86(3): 209-231.

Donald PF, Sanderson FJ, Burfield IJ, Bierman SM, Gregory RD, Waliczky Z (2007) International Conservation Policy Delivers Benefits for Birds in Europe. Science 317. https://doi.org/10.1126/science.1146002

Dudley N, Parrish JD, Redford KH, Stolton S (2010) The revised IUCN protected area management categories: the debate and ways forward. Oryx 44. https://doi.org/10.1017/S0030605310000566

Ervin J (2003) Protected Area Assessments in Perspective. BioScience 53. https://doi.org/10.1641/0006-3568(2003)053[0819:PAAIP]2.0.CO;2

Ervin J, Sekhran N, Dinu A, Gidda S, Vergeichik M, Mee J (2010) Protected Areas for the 21st Century: Lessons from UNDP/GEF's Portfolio. United Nations Development Programme and Montreal-Convention on Biological Diversity, New York, 1–129.

Gaston KJ, Jackson SF, Cantú-Salazar R, Cruz-Pinon G (2008) The ecological performance of protected areas. Annual Review of Ecology Evolution and Systematics 39. https://doi.org/10.1146/annurev.ecolsys.39.110707.173529

Gardenfors U (2001) Classifying threatened species at national versus global levels. Trends in Ecology and Evolution 16(9): https://doi.org/10.1016/S0169-5347(01)02214-5.

Grumbine ER (1994): What is ecosystem management? Conservation Biology 8: 27-38.

Herbert ME, McIntyre PB, Doran PJ, Allan JD, Abell R (2010) Terrestrial reserve networks do not adequately represent aquatic ecosystems. Conservation Biology 24. https://doi.org/10.1111/j.1523-1739.2010.01460.x

Hockings M, Stolton SW, Leverington F, Dudley N, Courrau J (2006) Evaluating effectiveness: A framework for assessing the management of protected areas (2nd edn). IUCN, Gland. https://doi.org/10.2305/IUCN.CH.2006.PAG.14.en

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. Ecological Letters 8: 23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x

Hromas J (2009) Caves in the Czech Republic. Agency of Nature Conservation and Landscape Protection,Prague, 1–608.

Jantke K, Schleupner C, Schneider UA (2011) Gap analysis of European wetland species: priority regions for expanding the Natura 2000 network. Biodiversity and Conservation 20(3). https://doi.org/10.1007/s10531-010-9968-9

Jenkins CN, Joppa L (2009) Expansion of the global terrestrial protected area system. Biological Conservation 142. https://doi.org/10.101016/j.biocon.2009.04.016

Joppa LN, Pfaff A (2009) High and Far: Biases in the location of protected areas. PLoS One 4(12). https://doi.org/10.1371/journal.pone.0008273

Kilianova H, Pechanec V, Brus J, Kirchner K, Machar I (2017) Analysis of the development of land use in the Morava River floodplain, with special emphasis on the landscape matrix. Moravian Geographical Reports 25(1). https://doi.org/10.1515/mgr-2017-0005

Kovarik Petr, Kutal M, Machar I (2014) Sheep and wolves: Is the occurrence of large predators a limiting factor for sheep grazing in the Czech Carpathians? Journal for Nature Conservation 22(5). https://doi.org/10.1016/j.jnc.2014.06.001

Kučera T (2012) Red List of Habitats in the Czech Republic. In: Machar I, Drobilova L (Eds) Ochrana prirody a krajiny v Ceske republice, vols I and II. Palacky University, Olomouc, 157–160. Accession Number: WOS:000334387900004

Leverington F, Costa KL, Pavese H, Lisle A, Hockings M (2010) A global analysis of protected area management effectiveness. Environmental Management 46. https://doi.org/10.1007/s00267-010-9564-5

Lipsky Z (1995) The changing face of the Czech rural landscape. Landscape and Urban Planning 31. https://doi.org/10.1016/0169-2046(94)01034-6

Loncakova J (2009) Habitat mapping as a base for SAC establishment. In: Handrij H, Loncakova J, Hosek M (Eds) Habitat mapping in the Czech Republic. Agency of Nature Conservation and Landscape Protection, Prague, 59–65.

Machar I (2009) Conservation and Management of Floodplain Forests in the Protected Landscape Area Litovelske Pomoravi (Czech Republic) Introduction. Palacky University, Olomouc, 7–108. [ISBN: 978-80-244-2355-5. Accession Number: WOS :000331015800001]

Machar I (2012) Protection of nature and landscapes in the Czech Republic Selected current issues and possibilities of their solution. In: Machar I, Drobilova L (Eds) Ochrana Prirody a Krajiny v Ceske Republice, vols I, II. Palacky University, Olomouc, 9. [Accession Number: WOS 000334387900001]

Machar I, Simon J, Rejsek K, Pechanec V, Brus J, Kilianova H (2016) Assessment of Forest Management in Protected Areas Based on Multidisciplinary Research. Forests 7(11): https://doi.org/10.3390/f7110285

Machar I, Vozenilek V, Kirchner K, Vlckova V, Bucek A (2017a) Biogeographic model of climate conditions for vegetation zones in Czechia. Geografie 122(1): 64–82. [Accession Number: WOS:000399065000004]

Machar I, Vlckova V, Bucek A, Vozenilek V, Salek L, Jerabkova L (2017b) Modelling of Climate Conditions in Forest Vegetation Zones as a Support Tool for Forest Management Strategy in European Beech Dominated Forests. Forests 8(3). https://doi.org/10.3390/f8030082

Machar I, Vozenilek V, Simon J, Pechanec V, Brus J, Fulnecek P, Vitek T (2017c) Joining of the historical research and future prediction as a support tool for the assessment of management strategy for European beech-dominated forests in protected areas. Nature Conservation 22: 51–78, https://doi.org/10.3897/natureconservation.22.12902

Maděra P, Machala M, Slach T, Friedl M, Černušáková L, Volařík D, Buček A (2017) Predicted occurrence of ancient coppice woodlands in the Czech Republic. iForest, 10. https://doi.org/10.3832/ifor2295-010

Margules C, Sarkar S (2007) Systematic Conservation Planning. Cambridge University Press, Cambridge, 1–270.

McDonald RI, Boucher TM (2011) Global development and the future of the protected area strategy. Biological Conservation 144. https://doi.org/10.1016/j.biocon.2010.09.016

Miko L (2012) Nature and landscape protection in the European context. In: Machar I, Drobilova L (Eds) Ochrana prirody a krajiny v Ceske republice, vols I and II. Palacky University, Olomouc, 43–49. [Accession Number: WOS:000334387900004]

Mittermeier RA, Mittermeier CG, Brooks THM, Pilgrim JD, Konstatnt WR, Da Fonseca GAB, Kormos C (2003) Wilderness and biodiversity conservation. Proceedings of the National Academy of Sciences of the United States of America 100. https://doi.org/10.1073/pnas.1732458100

Olson DM, Dinerstein E (2002) The Global 2000: Priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89(2). https://doi.org/10.2307/3298564

Oprsal Z, Kladivo P, Machar I (2016) The role of selected biophysical factors in long-term land-use change of cultural landscape. Applied Ecology and Environmental Research 14(2): 23–40. [Accession Number: WOS:000375222100002]

Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Tzungsu D, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Blackburn TM, Gaston KJ, Owens IPF (2005) Global hotspots of species richness are not congruent with endemism and threat. Nature 436: 1016–1019. https://doi.org/10.1038/nature03850

Pechanec V, Brus J, Kilianova H, Machar I (2015) Decision support tool for the evaluation of landscapes. Ecological Informatics 30: https://doi.org/10.1016/j.ecoinf.2015.06.006

Plesnik J (2012) International protection of nature and landscape. In: Machar I, Drobilova L (Eds) Ochrana prirody a krajiny v Ceske republice, vols I and II. Palacky University, Olomouc, 22-42. [Accession Number: WOS:000334387900004]

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. Bioscience 46. https://doi.org/10.2307/1312990

Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365. https://doi.org/10.1038/365335a0

Rodrigues ASL, Andelman S, Bakarr M, Boitani L, Brooks T, Cowling RM, Fishpool LDC, Da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004a) Effectiveness of the global protected area network in representing species diversity. Nature 428. https://doi.org/10.1038/nature02422

Rodrigues ASL, Akcakaya HR, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Chanson JS, Fishpool LDC, Da Fonseca GAB, Gaston KJ, Hoffmann M, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004b) Global gap analysis: Priority regions for expanding the global protected-area network. Bioscience 54(12). https://doi.org/10.1641/0006-3568(2004)054[1092:GGAPRF]2.0.CO;2

Ricketts TH, Dinerstein E, Boucher T, Brooks TM, Butchart SHM, Hoffmann M, Lamoreux JF, Morrison J, Parr M, Pilgrim JD, Rodrigues ASL, Sechrest W, Wallace GE, Berlin K, Bielby J, Burgess ND, Church DR, Cox N, Knox D, Loucks C, Luck GW, Master LL, Moore R, Naidoo R, Ridgely R, Schatz GE, Shire G, Strand H, Wettengel W, Wikramanayake E (2005) Pinpointing and preventing imminent extinctions. Proceedings of the National Academy of Sciences of the United States of America 102(51). https://doi.org/10.1073/pnas.0509060102

Romportl D, Chuman T, Lipsky Z (2013) Landscape typology of Czechia. Geografie 118(1): 16–39. Accession Number: WOS:000318255800002.

Sanderson FJ, Pople RG, Ieronymidou C, Burfield IJ, Gregory RD, Willis SG, Howard C, Stephens PA, Beresford AE, Donald PF (2015) Assessing the performance of EU nature legislation in protecting target bird species in an era of climate change. Conservation Letters. https://doi.org/10.1111/conl.12196

Santana J, Reino L, Stoate C, Borralho R (2013) Mixed effects of long-term conservation investment in Natura 2000 farmland. Conservation Letters 7. https://doi.org/10.1111/conl.12077

Simon J, Machar I, Bucek A (2014) Linking the historical research with the growth simulation model of hardwood floodplain forests. Polish Journal of Ecology 62(2): 273–288, https://doi.org/10.3161/104.062.0208

Stoll-Kleemann S (2010) Evaluation of management effectiveness in protected areas: Methodologies and results. Basic and Applied Ecology 11(5): 377–382. https://doi.org/10.1016/j.baae.2010.06.004

Skokanova H, Eremiasova R (2013) Landscape functionality in protected and unprotected areas: Case studies from the Czech Republic. Ecological Informatics 14. https://doi.org/10.1016/j.ecoinf.2012.11.007

Šenfeldr M, Maděra P (2011) Population Structure and Reproductive Strategy of Norway Spruce (Picea abies L. Karst) Above the Former Pastoral Timberline in the Hrubý Jeseník Mountains, Czech Republic. Mountain Research and Development 31. https://doi.org/10.1659/MRD-JOURNAL-D-10-00073.1

Tantipisanuh N, Savini T, Cutter P, Gale GA (2016) Biodiversity gap analysis of the protected area system of the Indo-Burma Hotspots and priorities for increasing biodiversity representation. Biological Conservation 195. https://doi.org/10.1016/j.biocon.2015.12.043

Turner WR, Brandon K, Brooks TM, Costanza R, da Fonseca GAB, Portela R (2007) Global conservation and biodiversity and ecosystem services. Bioscience 57. https://doi.org/10.1641/B571009

UNEP (2008) Report of the Ad Hoc Open-ended Group of UNEP on Protected Areas, Second Meeting, FAO Rome, 11-15 February 2008. Secretariat of the Convention on Biological Diversity, Montreal, 1–56.

Visconti P, Di Marco M, Alvarez-Romero JG, Januchowski-Hartley SR, Pressey RL, Weeks R, Rondinini C (2013): Effects of Errors and Gaps in Spatial Data Sets on Assessment of Conservation Progress. Conservation Biology 27(5). https://doi.org/10.1111/cobi.12095

Wesolowski T (2005) Virtual conservation: How the European Union is turning a blind eye to its vanishing primeval forests. Conservation Biology 19(5). https://doi.org/10.1111/j.1523-1739.2005.00265.x

Nature Conservation 24: 43–63 (2018)
doi: 10.3897/natureconservation.24.20607
http://natureconservation.pensoft.net

DATA PAPER

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Vector analysis: a tool for preventing the introduction of invasive alien species into protected areas

Gabriela I. E. Brancatelli[1], Sergio M. Zalba[1]

1 *GEKKO, Grupo de Estudios en Conservación y Manejo, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670 (8000), Bahía Blanca, Argentina*

Corresponding author: *Gabriela I. E. Brancatelli* (gabriela.brancatelli@uns.edu.ar)

Academic editor: *Y. Matsinos* | Received 25 August 2017 | Accepted 5 December 2017 | Published 4 January 2018

http://zoobank.org/48D0CD50-DC07-4548-9283-20534A075B29

Citation: Brancatelli GIE, Zalba SM (2018) Vector analysis: a tool for preventing the introduction of invasive alien species into protected areas. Nature Conservation 24: 43–63. https://doi.org/10.3897/natureconservation.24.20607

Abstract

Invasive alien species are the main agent of biodiversity loss in protected natural areas. Prevention is the most appropriate management tool for addressing this challenge, however, virtually all ongoing management efforts are focused on established populations. Although invasion processes include stochastic components, it is possible to compare the different vectors of introduction that operate in a particular area in terms of their potential to transport species of high risk of invasion efficiently and, once identified, to establish strategies of prevention, early detection and rapid action. This study proposes a system of prioritization of vectors of alien plant dispersal for optimizing the efforts for preventing invasion. The system was developed for the Ernesto Tornquist Provincial Park (province of Buenos Aires, Argentina), but it is directly applicable to other areas. Natural and anthropogenic vectors were evaluated and lists of the species potentially transported by each vector were elaborated according to the characteristics of their propagules. The system analyzes the relative importance of each vector according to: 1) the severity of the potential impact of transportable species, 2) the difficulty of controlling these species, and 3) the volume of transportable propagules. In the case under study, the maximum value of risk corresponds to cargo, followed by vehicles, streams, unintentional human transport, intentional human transport, wind and finally, animals. This analysis can lead to prevention strategies, mapping of dispersal routes and actions of early detection and rapid response.

Keywords

biological invasions, pathways, prevention, protected areas, vectors

Introduction

The impact of invasive alien species is a key component of global change and it is considered one of the main causes of biodiversity loss worldwide (Sala et al. 2000, Lövei and Lewinsohn 2012, Simberloff et al. 2013, Alexander et al. 2014). All protected natural areas contain alien species that are recognized as the main threat to their conservation objectives. Predictions indicate that their importance will increase in the future unless effective management measures are adopted (McKinney 2002, Pyšek et al. 2002). The effects of invasions can be manifested at different scales and in various ways, including reduction in the richness and abundance of species of the native biota, genetic changes in native populations through hybridization and interruptions in mutualistic networks (Pyšek et al. 2012). In some cases, the effects of the presence of one or more invasive species are so profound that they disrupt the functioning of entire ecosystems and interfere with their resilience and ability to provide ecosystem services (Vilà et al. 2011, Simberloff et al. 2013).

Invasion processes involve the successful overcoming of several challenges: a potential invader must survive transport from its place of origin, become established in the new site, persist and reproduce until a sustainable population is formed that eventually expands (Theoharides and Dukes 2007, Blackburn et al. 2011, Jeschke et al. 2013). The ability to successfully overcome these stages depends not only on the species' own characteristics, but also on the characteristics of the invaded habitat that determine its susceptibility to invasion, the number of propagules and introduction events, the establishment of effective relationships with local dispersal agents and other symbionts and the particular conditions at the time of the arrival of the propagules (Marco et al. 2002, Colautti et al. 2006, Dechoum et al. 2015, Amodeo and Zalba 2017).

The management of invasive alien species includes four basic components: prevention, early detection, eradication and control that coincide with each stage of the invasion process (Wittenberg and Cock 2001, Lodge et al. 2006, Davies and Sheley 2007). The best cost-effective method for dealing with invasive alien species is in the area of prevention, since the costs and impacts generated by an invasion process increase and sometimes the problems become irreversible (Leung et al. 2002, Ziller and Zalba 2007, Anderson et al. 2014).

Vectors are the transfer mechanisms responsible for the introduction and spread of invasive species in a certain area, including a wide variety of physical means or agents, from ballast water to horticulture, biological control and aquaculture (Ruiz and Carlton 2003). Vector interception or disruption has been identified as "the most vulnerable and directly manageable portion of the invasion sequence", as they allow to simultaneously avoid the delivery of whole sets of transportable species (Carlton and Ruiz 2005).

Many risk analysis associated to the probabilities of introduction by certain vectors has been developed, mostly at national or state borders (Gordon et al. 2012, Grosholz et al. 2012, Conser 2013, Kelly et al. 2013). Most of them consider the capacity of the vectors to safely transport propagules, the volume that can be carried and the frequency of operation, as well as the impacts associated to the transportable taxa. This is not the case for protected areas, where these kind of analysis are extremely infrequent. Despite the consensus on the disproportionate importance of prevention in the management of biological invasions, most management actions developed in nature reserves focus on the control or eradication of established populations (Schüttler and Karez 2008, Genovesi and Monaco 2013, Pauchard et al. 2015). This situation could be explained, at least in part, since the extent and seriousness of the problems attract the attention of those responsible for the management of the reserves disproportionately. Apart from the causes of this scenario, the consequences seem clear: the lack of effective preventive actions compromises the sustainability of protected areas that face the threat of invasive alien species.

Moreover, the scarcity of tools for organizing actions that reduce the risk of introduction and establishment of new species is daunting (Davies and Sheley 2007). Although invasion processes include stochastic components, like the co-occurrence of propagule arrival and appropriate environmental conditions for establishment (Radford 2013), it is likely to anticipate which species are most likely to arrive in an area, the severity of their potential impacts, the most likely means of arrival, and which sites are most likely to be colonized. In particular, it is possible to compare the different vectors of introduction operating in a given area in terms of their potential to transport highly invasive species efficiently.

Vectors also travel through more or less predictable routes known as pathways (Mack et al. 2003). The combination of knowledge about vectors with higher chances of transporting high risk species and the routes that they travel to and within a particular area leads to the organization of preventive actions, early detection and rapid action (Lodge et al. 2006, Ziller and Zalba 2007). This alternative also has the advantage of simultaneously addressing the risk of introduction of complete sets of species sharing the same means of transport and / or pathways of introduction and dispersion.

The objective of this study is to create a system of risk analysis for the introduction of invasive or potentially invasive alien plants by identifying the vectors of the highest priority for control. We selected the Ernesto Tornquist Provincial Park, a nature reserve located in the southern part of the Pampas Biome, in the Argentine Republic, as a case of analysis for the elaboration and application of this system. The park is dominated by grass steppes and surrounded by an agricultural landscape. Vectors of plant dispersal in the area include physical means like wind and watercourses, dispersal by birds, mammals and invertebrates, and human mediated spread in association to footwear and clothing, vehicles and cargo (Zalba and Villamil 2002, Loydi and Zalba 2009, Amodeo and Zalba 2013).

The reserve undergoes intense invasions by alien species, including different species of trees and shrubs (Zalba and Villamil 2002, Zalba et al. 2009). Apart from this problem, there is a high number of introduced plant species in the region that have not yet become established in the reserve (Long and Grassini 1997), and preventing their entry should be a priority in the management of the area. The analysis of routes and vectors is an appropriate response to reduce the impact of invasive species by minimizing the risks of introduction, as well as lowering the very high costs associated with the control.

Materials and methods

Study area

The Pampas biome is one of the most characteristic landscapes in southern South America, as well as being one of the most greatly transformed ecosystems by anthropogenic actions, with only a very small area that is protected effectively (Bertonatti et al. 2000, Bilenca and Miñarro 2004). The grasslands of South America face a serious and increasing challenge associated with the progress of invasive alien species, particularly woody plants (Fonseca et al. 2013). The Ernesto Tornquist Provincial Park (ETPP) represents one of the few protected areas of Pampas grassland in Argentina (Bilenca and Miñarro 2004, De Villalobos and Zalba 2010). The reserve covers an area of approximately 6700 ha in the central area of Sierra de la Ventana, in the province of Buenos Aires, Argentina (38°3.90'S, 61°58.33'W). The climate in the region is temperate and rainfall varies between 500 and 800 mm annually (Burgos 1968). The vegetation is dominated by grass steppes, including species of *Stipa*, *Nassella*, *Piptochaetium*, and *Festuca*, as well as herbs and shrubs of Asteraceae. The flora of the park includes some 550 species of native plants and some 140 alien species (Long and Grassini 1997, Long et al. 2004).

Damiani (2007) cites a total of 324 alien plant species growing within the ETPP and in an area of about 20 km around it, including agricultural and livestock fields, paved roads, secondary roads, and parks and gardens in small villages. Twenty-three species that behave as invasive in the area, extensively growing over natural and semi natural environments, and 23 others that can be considered to be of high risk on account of their biological characteristics and previous invasive behavior, have not yet been detected in ETPP, or are restricted to intensive use zones (Damiani 2007, Long and Grassini 1997, María Andrea Long, Systematic Botany, Universidad Nacional del Sur, pers. comm.). All these species can therefore be considered as high priority in a prevention strategy (Appendix 1).

Methods

The characteristics of the propagules (presence of wings, pappus, hooks, sweet pulp, etc.) and dispersal strategies of the 46 species considered to be of high priority for prevention were analyzed from the literature and the vectors that might intervene in their dispersion were identified.

In order to analyze the relative importance of each vector, the severity of the potential impact and the difficulty of controlling each transportable species were taken into account, as well as the volume of propagules that the vector could carry.

The potential impact of the vector index (PIV) was defined as the weighted sum of the number of species transportable by a vector for each category of potential impact:

PIV = 100 * number of species with high PI + 10 * number of species with medium PI + number of species with low PI.

The values of high, medium and low potential impact were taken from Damiani (2007), who established an impact index considering the risk of establishment of the species based on fourteen criteria: previous invasive behavior, niche width, density of growth, hybridization risk, allelopathy, toxicity for humans, toxicity for wildlife, flammability (capacity to increase fire frequency or intensity), palatability, capacity to host parasites and pathogens, life cycle, reproductive strategy, seed production and dispersal. Each criterion has different alternatives associated with corresponding numeric values that are combined in a final estimation of potential impact of the species.

The control difficulty index of the species transported by the vector **(CDV)** was defined as the weighted sum of the number of species transportable by the said vector corresponding to each category of control difficulty:

CDV = 100 * number of species with high CD + 10 * number of species with mean CD + number of species with low CD.

The values of high, medium and low control difficulty were also extracted from Damiani (2007), who calculated them considering six species features: presence of spines and stinging hairs, generation time, ability to regrow after cutting, response to grazing, response to fire, and persistence in the seed bank. Numerical indexes for each criterion were combined to assess the difficulty to control each species.

The severity of impact of each vector (SI) was calculated from the values of the potential impact and control difficulty indexes of the species transported by the vector, according to:

SI = (PIV + CDV) / SImax

Where SImax represents the maximum severity of impact obtained among the considered vectors.

The Transportable Volume **(TV)** was estimated by analyzing both the number of propagules available for transport (TP) and the carrying capacity of the vector (CC).

The number of available propagules (TP) for each vector was calculated by combining the information related to the abundance of the species in the area with the production and temporal availability of transportable propagules by that vector.

The abundance of each species in the study area was estimated on a relative scale, assigning a value of 1 to the rare species (few populations of a few individuals), the value of 2 to the abundant species (few populations with many individuals or many populations with few individuals) and the value of 3 to very abundant species (many populations with many individuals). This information was obtained from literature (Long and Grassini 1997) and from consultations with specialists of the regional flora. The number of propagules produced by each species was classified as low (1), moderate

(2), high (3) or very high (4), considering the ability of an adult plant to produce seeds and / or vegetative reproduction structures (bulbs, rhizomes, stolons, tubers and plant cuttings). This data was extracted from the bibliography. The proportion of months in the year during which the propagules of each species are available for eventual transport by each vector was also determined. Thus, for example, a plant producing fleshy fruits available for consumption and dispersal by vertebrates for two months each year would obtain a value of 2/12 = 0.17 for the animal vector; whereas we could expect an availability of 12/12 = 1 for vector loads, if their seeds remain viable in the soil.

These three variables were multiplied by each other to calculate the abundance of propagules for each species. The abundance values of propagules for all transportable species were added to obtain the total number of propagules available for transport by each vector (TP).

Two variables were considered for estimating the carrying capacity of each vector (CC): 1- the volume transported in each potential introduction event, defined in relative units: 1 small; 10 medium; 100 large; 1000 very large, and 2- the frequency of vector activity throughout the year in the study area, expressed in relative units: 1 low; 10 medium; 100 high; 1000 very high.

These two variables were multiplied to calculate the carrying capacity (CC) of each vector.

The transportable volume (TV) per vector was calculated by adding the propagation availability and carrying capacity:

$$TV = (TP + CC) / TVmax$$

Where TVmax represents the volume of transportable propagules by the vector with the greatest transport capacity.

Finally, the values of impact severity (SI) and transportable volume (TV) were combined to calculate the risk associated with each vector (RV):

$$RV = (2 * SI + TV) / 3$$

The impact severity value was multiplied by 2 to reflect its relative importance when analyzing the risk associated with each vector.

A diagram of this analysis is presented in Fig. 1.

Results

The analysis of the propagules and dispersal strategies of the species of high priority of prevention in the PPET allowed us to associate them with a total of three natural and three anthropogenic vectors. The natural vectors identified were streams, wildlife and wind. The anthropogenic vectors included transport by vehicles (in mud attached to the chassis and tyres), movement directly associated with people (unintentional: in

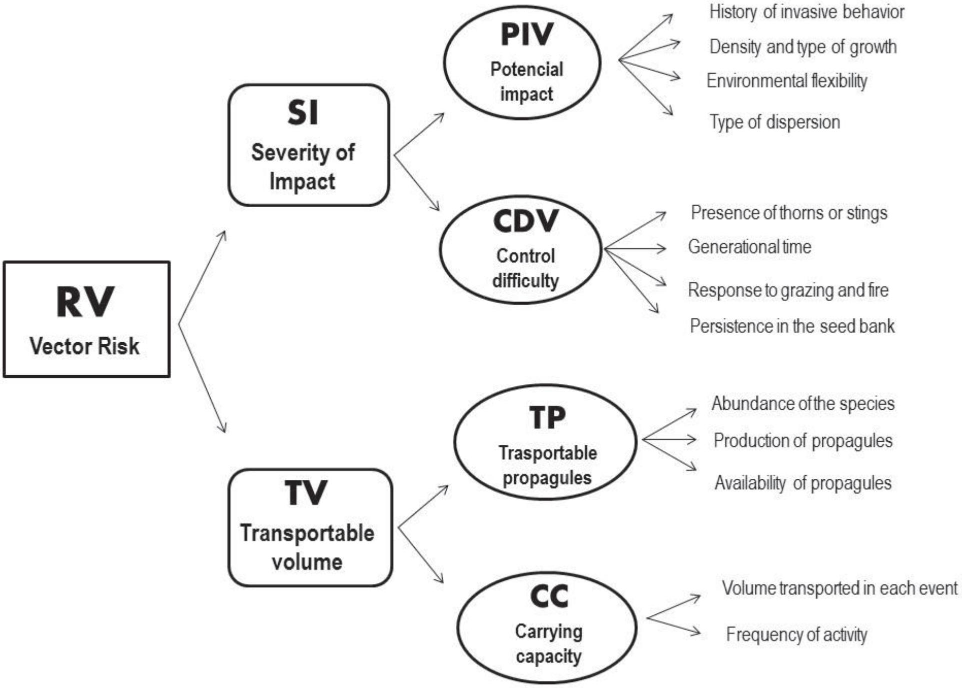

Figure 1. Vector analysis schema. Diagram of the analysis of the relative importance of vectors associated with the introduction and dispersal of invasive alien plants in Ernesto Tornquist Provincial Park (Buenos Aires, Argentina).

footwear and clothing, food, camping equipment, and intentional: ornamental plants and vegetables) and the movement associated with cargo (soil, sand, debris, and dry plant material).

Of the 46 species evaluated, 25 have propagules with structures that facilitate their dispersion by wind (e.g. small and light seeds, winged diasporas, feathery organs), 7 show seeds with traits that promote their dispersal by water (light seeds or floating vegetative structures) and 13 fruits are potentially dispersed by animals (edible or with hooks, barbs or awns that adhere to fur). We also concluded that all the propagules of the analyzed species could be transported in loads of materials (earth, debris, sand), whereas 39 show traits that would facilitate their transport by cars, trucks and other vehicles (small seeds, adherent propagules). Twenty-eight species could be easily dispersed directly and unintentionally by people (on footwear and clothing, such as fruits of food plants or associated with camping equipment). Finally, 23 species could be intentionally mobilized by the people for their ornamental value or cultivation for other human purposes (Appendix 1, Fig. 2A).

The analysis of the different vectors, combining the potential impact of the transportable species (Damiani 2007), resulted in an index of the potential impact of the vector that varied between 240 and 1693. On the other hand, the index of the difficulty of control of species transported by the vector takes values that go between 321 and 1891.

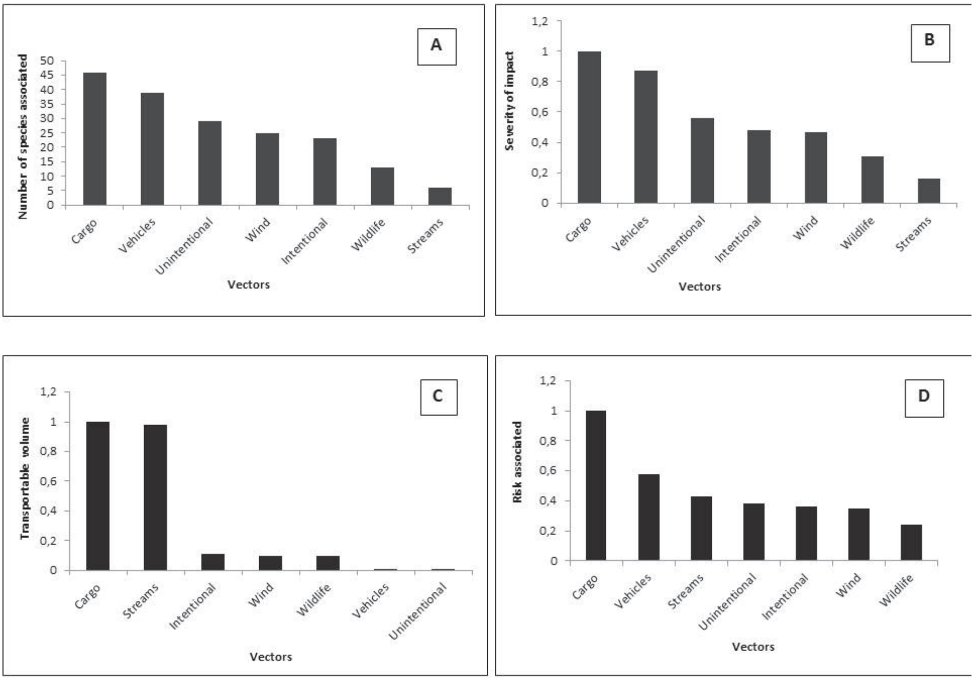

Figure 2. Vectors of introduction and spread of invasive and potentially invasive alien plants present in intensive use zones of the Ernesto Tornquist Provincial Park and it's surroundings (Buenos Aires, Argentina). **A** Number of species associated to each dispersion vector according to the characteristics of their fruits and seeds and their human use **B** Severity of impact of vectors depending on the potential impact of transportable species and the difficulty of their control **C** Relative capacity of vectors to transport propagules **D** Risk associated with vectors depending on the potential impact of transportable species, the difficulty of their control and the transport capacity of the vector.

In both cases, the maximum value corresponds to cargos and the smaller one to streams. Thus, the severity of impact of the vector index was maximized for cargo (1), followed by vehicles (0.87), unintentional human transport (0.56), intentional human transport (0.48), wind (0.47), wildlife (0.31) and streams (0.16) (Fig. 2B).

Regarding the transport capacity of the different vectors, the transportable propagules index varied between 11 and 226, again reaching the maximum value for cargo and the minimum for streams.

Twenty species were evaluated as very abundant, 16 as abundant and 10 as rare. A high number of propagules were produced by 30.4% of the species under study, moderate production by 50% and a low number of propagules by eight species (17.4%). Only one species (*Melia azedarach*) was considered as having a very high production of propagules.

It was defined that propagules of all plants that can be transported in association with cargo or intentionally by humans are available for these vectors for 12 months per year. Vehicles and unintentional human transport might transport species with available propagules for periods of two to five months per year; whereas animals and

Table 1. Vectors characterization. Potential impact (PIV), control difficulty (CDV), severity of impact (SI), transportable propagules (TP), individual transport capacity, activity frequency, carrying capacity (CC), transportable volume (TV) and resulting risk (RV) for vectors capable of transporting invasive and potentially invasive alien plants present in intensive use zones of the Ernesto Tornquist Provincial Park and it's surroundings (Buenos Aires, Argentina).

	Cargo	**Vehicles**	**Streams**	**Unintencional by people**	**Intentional by people**	**Wind**	**Wildlife**
PIV	1693	1461	240	1081	833	871	481
CDV	1891	1659	321	937	896	817	643
SI	1	087	0.16	0.56	0.48	0.47	0.31
TP	226	53.08	11	35.17	101.10	13	16.42
Indiv. Capacity	1000	10	1000	1	1000	1	10
Frequency	10	10	10	100	1	1000	100
CC	10000	100	10000	100	1000	1000	1000
TV	1	0.01	0.98	0.01	0.11	0.11	0.11
RV	1	0.58	0.43	0.38	0.36	0.35	0.24

streams could transport species with available propagules between one and 12 months per year. The wind vector could disperse species with available propagules between one and three months per year.

The carrying capacity, for its part, was considered maximum for the cargo, stream and wind vectors, whereas the minimum value was for the vehicle and unintentional human transport vectors.

The volume transported at each potential introduction event was considered to be very large for cargo, streams, wind and intentional human transport; medium for vehicles and animals and small for unintentional human transport.

Only intentional human transport was considered to have a very low frequency of activity. For unintentional transport by humans and mediated by animals, the frequency is considered high, whereas it is classified as medium for cargo, wind, vehicles and streams.

Thus, the transportable volume index resulted maximum for cargo (1), followed immediately by streams and wind (0.98), whereas the rest of the vectors received values of ten to one hundred times lower in terms of their relative transport capacity (Fig. 2C).

The combination of the information described allowed us to calculate the risk associated with each vector, being maximum for cargo (1), followed by vehicles (0.58) and streams (0.43), unintentional human transport (0.38), intentional human transport (0.36), wind (0.35) and wildlife (0.24) (Fig. 2D, Table 1).

Discussion

In this study, we designed and applied a risk analysis system associated with vectors responsible for the introduction and dispersal of plant species, which constitutes a simple and novel alternative of high potential value for decreasing the risk associated to invasive species by reducing propagule pressure in a variety of ways: improving detection measures and border policies, limiting vector contamination, controlling invasive populations in source regions, helping to raise public awareness of problems to find alternatives for invasive species (Pyšek and Richardson 2010). As we previously mentioned, there are many antecedents aimed at reducing unwanted introductions by assessing the risk associated with vectors and pathways, most of them applied at national or state borders (Gordon et al. 2012, Grosholz et al. 2012, Conser 2013, Kelly et al. 2013). The main differences of our approach include it local focus, primarily designed for individual reserves, what can result in an improvement of the precision of the analysis. It is also based on a context-specific perspective that drives the attention of the administrators to real threats posed by potentially invasive species that are present in the surroundings.

As discussed in detail below, the ranking obtained in this work is consistent with particular features of our case study, including heavy transit of vehicles associated to tourism and cargo, strong and frequent winds (particularly during plant dispersal seasons), and a dense network of water courses. This situation will clearly change in other reserves, but the framework should still be useful to calculate a specific scoring of dispersal vectors.

The development of an index of the relative importance of vectors of introduction and dispersal presents some challenges, such as comparing vectors as different from each other as the wind and the sole of a shoe. Another weakness associated with this index is related to its need of information about the presence of invasive or potentially invasive species in the area surrounding the reserve that could be not available in some cases. On the other hand, data on previous invasive behavior of the species of interest is becoming easier to obtain with growing regional and national databases on invasive species. Something similar occurs with the characteristics of the species that permit to associate them to dispersal vectors, as most of the potentially invasive plants are regionally or even globally shared (Randall 2017). It is also important to recognize that the invasion process is dynamic and that some of the species that are classified as non-invasive at one time could become aggressive invaders if there are changes in the environmental conditions or the invasive population itself (Davis et al. 2000, Jiménez et al. 2011, Dechoum et al. 2014, Schrama and Bardgett 2016), possibly affecting the relative importance of the different vectors under analysis. It is therefore advisable to update the lists of species to be included in the analysis periodically.

Apart from the specific function of this analysis, the structure of the proposed indexes allows us to separate the different components associated with the potential impact of each vector and this could guide actions for reducing their potential impact on the area (Davies and Sheley 2007). Thus, management actions could be oriented, alternatively or complementarily, towards reducing the frequency or capacity of the individual transport of a vector, controlling its effects during periods of availability of transportable propagules and avoiding the transport of high risk species (e.g., through the elimination of the foci of invasion at the origin or in the path that a vector travels), etc. The structure of this system would also enable to evaluate more specific dispersal vectors (for example bicycles vs. walking or horseback riding), opening up interesting opportunities for the zoning and management of protected areas against the challenge of invasive alien species.

The vectors analyzed in our case study are clearly separated into two groups: on the one hand the anthropogenic agents (cargo, vehicles and intentional and unintentional transport by people) and, on the other hand, the natural means of dispersal (water, wind and animals). Due to their intrinsic characteristics, these two sets of vectors are associated with different and complementary management strategies, while the former allow and justify control and preventive actions; the latter are more naturally associated with early detection, since it is difficult or directly not feasible to reduce their transport capacity.

The results of the analysis place the vectors of cargo and transport associated with vehicles among the highest risks of entry of potentially invasive plant species in the study area. A number of studies have shown that unintentional transport by vehicles, either associated directly to the vehicle, or with cargo, is an important mechanism of seed dispersal (Clifford 1959, Lonsdale and Lane 1994, Von Der Lippe and Kowarik 2007, Ansong and Pickering 2013). The climatic conditions, the season of the year, the place where it is driven and the parts of the vehicle exposed to the environment affect this type of dispersal; as well as the weight and size of the seeds and the place where it is loaded (Zwaenepoel et al. 2006, Von der Lippe and Kowarik 2008, Veldman and Putz 2010, Taylor et al. 2012). While the relative importance of vehicles and transported freight is likely to vary between reserves, their particular relevance has an encouraging aspect, considering that the points of entry of freight vehicles and passenger cars are often few in number and are well defined, and that the same is true for the dispersal routes of these vectors within the reserves (internal roads and parking areas). The cleaning of vehicles before entering the area has proven to be an efficient measure for reducing the amount of propagules transported. The duration and type of washing will depend on the size and shape of the vehicle (Rew and Fleming 2011). Other preventive measures could include restricting vehicular traffic or creating invasive species free zones along roadsides (Davies and Sheley 2007). The handling of cargo allows specific actions, including quarantine systems (temporary deposit of the material entered in safe places that allow the detection and elimination of species that could germinate and settle there). There is also the option of evaluating the sites of origin of the materials, avoiding those affected by invasions of species transportable by this vector, in addition to thoroughly cleaning the containers before loading. These preventive measures should be complemented with periodic surveys along the internal roads in search of plants that might have entered these pathways, and their immediate removal (Lee and Chown 2009).

The wind vector represents a particular challenge (Davies and Sheley 2007) and preventive actions could be aimed at eliminating nuclei of transportable species located on the windward side of the reserve. If this were not possible, areas of high risk of invasion could be defined depending on the location of these nuclei and the prevailing winds during the months of seed production, which should be subject to regular monitoring and control tasks.

Streams as vectors follow in the order of risk. In this case the preventive measures are more complex and the effort should be directed at monitoring of the banks in search of points of entry of species (Cabra-Rivas et al. 2014). In general terms, the search actions should focus on streams that correspond to watersheds originating outside the reserve, concentrating the training efforts of personnel dedicated to detection on the set of species transportable by this vector, which clearly increases the chances of an efficient identification. In addition, resources could be devoted to the detection of nuclei of these species in sectors of the watershed located outside the reserve, where eradication would act as an efficient preventive measure that would save efforts and resources for the detection and control of internal foci of invasion (Säumel and Kowarik 2010).

The management of intentional and unintentional anthropogenic transport vectors includes a significant component of education and awareness. In the case of the former, it is essentially a question of avoiding the use of potentially invasive plant species in the staff residences and in the recreation areas (parks, gardens, shade trees) and replacing high risk plants in these sites. The unintentional transportation in clothing, footwear, backpacks, or other personal items have been documented in numerous studies (e.g. Whinam et al. 2005, McNeill et al. 2008, Pickering and Mount 2010, Auffret and Cousins 2013). Some reserves regulate the number of visitors and the period of access to reduce the unwanted introduction of propagules. There are natural protected areas in U.S.A. and New Zealand that require footwear, clothing, vehicles and equipment to be cleaned prior to entry (Genovesi and Monaco 2013). Researchers and park rangers pose a particularly high risk as they go to areas that are not accessible to the public, including areas of special conservation value (Chown et al. 2012, Huiskes et al. 2014).

The control of dispersal by animals leaves an even smaller space for prevention tasks, but could motivate monitoring tasks at sites with greater frequency of use by agents of high dispersal efficiency (e.g., wire fences or trees used as perches by frugivorous birds, Gosper et al. 2005, Buckley et al. 2006, Amodeo and Zalba 2013).

Making a list of high-risk species for each place and adapting the vectors that transport them, the analysis developed in this paper can be applied to other protected areas, political units or as a basis for the allocation of prevention efforts, early detection and early control of invasive species, translating the prevention premises frequently seen in the literature on biological invasions into concrete actions.

Aknowledgements

This work was supported by the National Scientific and Technical Research Council (CONICET), Argentina and Universidad Nacional del Sur, Bahía Blanca, Argentina. We are grateful to the Ernesto Tornquist Provincial Park rangers and authorities and to Rosemary Scoffield and Nicolás D´Onofrio for language revision.

References

Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biology Letters 10: 20130946. http://dx.doi.org/10.1098/rsbl.2013.0946

Amodeo MR, Zalba SM (2013) Wild cherries invading natural grasslands: unraveling colonization history from population structure and spatial patterns. Plant Ecology 214: 1299–1307. https://link.springer.com/article/10.1007/s11258-013-0252-4

Amodeo MR, Vázquez MB, Zalba SM (2017) Generalist dispersers promote germination of an alien fleshy-fruited tree invading natural grasslands. PLoS One 12: e0172423. http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0172423

Amodeo MR, Zalba SM (2017) Sex morphs and invasiveness of a fleshy-fruited tree in natural grasslands from Argentina. Botany 95(9): 913–922. https://doi.org/10.1139/cjb-2017-0041

Anderson LG, White PC, Stebbing PD, Stentiford GD, Dunn AM (2014) Biosecurity and vector behaviour: evaluating the potential threat posed by anglers and canoeists as pathways for the spread of invasive non-native species and pathogens. PLoS One 9: e92788. https://doi.org/10.1371/journal.pone.0092788

Ansong M, Pickering C (2013) Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. PLoS One 8: e80275. https://doi.org/10.1371/journal.pone.0080275

Auffret AG, Cousins SAO (2013) Humans as long-distance dispersers of rural plant communities. PLoS One 8(5): e62763. https://doi.org/10.1371/journal.pone.0062763

Azpiroz AB, Isacch JP, Dias RA, Di Giacomo AS, Fontana CS, Palarea CM (2012) Ecology and conservation of grassland birds in southeastern South America: a review. Journal of Field Ornithology 83:217–246. https://doi.org/10.1111/j.1557-9263.2012.00372.x

Bertonatti C, Corcuera J (2000) Situación ambiental argentina 2000. Fundación Vida Silvestre, Buenos Aires, 1–440.

Bilenca D, Miñarro F (2004) Identificación de áreas valiosas de pastizal en las pampas y campos de Argentina, Uruguay y sur de Brasil. Fundación Vida Silvestre, Buenos Aires, 352 pp.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in ecology & evolution 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Buckley YM, Anderson S, Catterall CP, Corlett RT, Engel T, Gosper CR, Nathan R, Richardson DM, Setter M, Spiegel O et al. (2006) Management of plant invasions mediated by frugivore interactions. Journal of Applied Ecology 43: 848–857. https://doi.org/10.1111/j.1365-2664.2006.01210.x

Burgos J (1968) El clima de la Provincia de Buenos Aires en relación con la vegetación natural y el suelo. In: Cabrera AL (Ed.) Flora de la provincia de Buenos Aires. Colección Científica del INTA 4(1) (Buenos Aires): 33–100.

Cabra-Rivas I, Alonso Á, Castro-Díez P (2014) Does stream structure affect dispersal by water? A case study of the invasive tree *Ailanthus altissima* in Spain. Management of Biological Invasions 5: 179–186. https://doi.org/10.3391/mbi.2014.5.2.11

Carlton J, Ruiz G (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. Chapter 3. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (Eds) Invasive Alien Species: A New Synthesis. Island Press, Washington DC, 36–58.

Chown SL, Huiskes AHL, Gremmen NJM, Lee JE, Terauds A, Crosbie K, Frenot Y, Hughes KA, Imura S, Kiefer K et al. (2012) Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. Proceedings of the National Academy of Sciences 109: 4938–4943. https://doi.org/10.1073/pnas.1119787109

Clifford HT (1959) Seed dispersal by motor vehicles. Journal of Ecology 47: 311–315. https://doi.org/10.2307/2257368

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: A null model for biological invasions. Biological Invasions 8: 1023–1037. https://doi.org/10.1007/s10530-005-3735-y

Conser C (2013) Invasive Species Pathway Risk Analysis for California. University of California, Davis, 1–97. http://www.iscc.ca.gov/docs/reports/CISAC-Pathway-Report-July-2013-web.pdf

Damiani ML (2007) Plantas exóticas en Sierra de la Ventana (Buenos Aires): detección de invasores potenciales. PhD Thesis, Universidad Nacional del Sur, Bahía Blanca.

Davies KW, Sheley RL (2007) A conceptual framework for preventing the spatial dispersal of invasive plants. Weed Science 55: 178–184. https://doi.org/10.1614/WS-06-161

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dechoum MS, Castellani TT, Zalba SM, Rejmánek M, Peroni N, Tamashiro JY (2014) Community structure, succession and invasibility in a seasonal deciduous forest in southern Brazil. Biological Invasions 17: 1697–1712. https://doi.org/10.1007/s10530-014-0827-6

Dechoum MS, Rejmánek M, Castellani TT, Zalba SM (2015) Limited seed dispersal may explain differences in forest colonization by the Japanese raisin tree (*Hovenia dulcis* Thunb.), an invasive alien tree in Southern Brazil. Tropical Conservation Science 8: 610–622. https://doi.org/10.1177/194008291500800303

De Villalobos A, Zalba SM (2010) Continuous feral horse grazing and grazing exclusion in mountain pampean grasslands in Argentina. Acta Oecologica 36: 514–519. https://doi.org/10.1016/j.actao.2010.07.004

Fonseca CR, Guadagnin DL, Emer C, Masciadri S, Germain P, Zalba SM (2013) Invasive alien plants in the Pampas grasslands: a tri-national cooperation challenge. Biological Invasions 15: 1751–1763. https://doi.org/10.1007/s10530-013-0406-2

Genovesi P, Monaco A (2013) Guidelines for addressing invasive species in protected areas. In Plant Invasions in Protected Areas. In: Foxcroft L, Pyšek P, Richardson DM, Genovesi P (Eds) Plant Invasions in Protected Areas: Patterns, Problems and Challenges, Invading Nature. Springer Series in Invasion Ecology 7: 487–506. https://doi.org/10.1007/978-94-007-7750-7_22

Gosper CR, Stansbury CD, Vivian-Smith G (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. Diversity and Distributions 11: 549–558. https://doi.org/10.1111/j.1366-9516.2005.00195.x

Gordon DR, Gantz CA, Jerde CL, Chadderton WL, Keller RP, Champion PD (2012) Weed Risk Assessment for Aquatic Plants: Modification of a New Zealand System for the United States. Plos One 7: e40031. https://doi.org/10.1371/journal.pone.0040031

Grosholz E, Crafton RE, Fontana RE, Pasari J, Williams S, Zabin C (2012) Aquatic Invasive Species Vector Risk Assessments: An Analysis of Aquaculture as a Vector for Introduced Marine and Estuarine Species in California.University of California Davis, 1–77. http://www.opc.ca.gov/webmaster/ftp/project_pages/AIS/AIS_Aquaculture.pdf

Huiskes AH, Gremmen NJ, Bergstrom DM, Frenot Y, Hughes KA, Imura S, Kiefer K, Lebouvier M, Lee JE, Tsujimoto M (2014) Aliens in Antarctica: assessing transfer of plant propagules by human visitors to reduce invasion risk. Biological Conservation 171: 278–284. https://doi.org/10.1016/j.biocon.2014.01.038

Jeschke JM, Keesing F, Ostfeld RS (2013) Novel Organisms: comparing invasive species, GMOs, and emerging pathogens. AMBIO 42: 541–548. https://doi.org/10.1007/s13280-013-0387-5

Jiménez MA, Jaksic FM, Armesto JJ, Gaxiola A, Meserve PL, Kelt DA, Gutiérrez JR (2011) Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. Ecology Letters 14: 1227–1235. https://doi.org/10.1111/j.1461-0248.2011.01693.x

Kelly J, O'Flynn C, Maguire C (2013). Risk analysis and prioritisation for invasive and non-native species in Ireland and Northern Ireland. Report prepared for the Northern Ireland Environment Agency and National Parks and Wildlife Service as part of Invasive Species Ireland, 1–59. http://invasivespeciesireland.com/wp-content/uploads/2013/03/Risk-analysis-and-prioritization-29032012-FINAL.pdf

Lee JE, Chown SL (2009) Breaching the dispersal barrier to invasion: quantification and management. Ecological Applications 19: 1944–1959. https://doi.org/10.1890/08-2157.1

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London B: Biological Sciences 269: 2407–2413. https://doi.org/10.1098/rspb.2002.2179

Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA et al. (2006) Biological Invasions: Recommendations for U.S. Policy and Management.. Ecological Applications 16: 2035–2054. https://doi.org/10.1890/1051-0761(2006)016[2035:BIRFUP]2.0.CO;2

Loydi A, Zalba SM (2009) Feral horses dung piles as invasion windows in natural grasslands. Plant Ecology 201(2): 471–480. https://doi.org/10.1007/s11258-008-9468-0

Long MA, Grassini CM (1997) Actualización del Conocimiento Florístico del Parque Provincia E. Tornquist. Buenos Aires, Argentina. Final Report Ministerio de Asunto Agrarios, Provincia de Buenos Aires and Universidad Nacional del Sur,Bahía Blanca, 276 pp.

Long MA, Peter G, Villamil CB (2004) La familia Asteraceae en el sistema de Ventania (Buenos Aires, Argentina). Boletín Sociedad Argentina de Botánica 39: 159–169.

Lonsdale WM, Lane AM (1994) Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. Biological Conservation 69: 277–283. https://doi.org/10.1016/0006-3207(94)90427-8

Lövei GL, Lewinsohn TM (2012) Megadiverse developing countries face huge risks from invasives. Trends in Ecology & Evolution 27: 2–3. https://doi.org/10.1016/j.tree.2011.10.009

Mack RN, Ruiz G, Carlton J (2003) Global plant dispersal, naturalization, and invasion: pathways, modes, and circumstances. In: Ruiz G, Carlton J (Eds) Invasive species: Vectors and management strategies. Island Press,Washington, 3–30.

Marco DE, Páez SA, Cannas SA (2002) Species Invasiveness in Biological Invasions: A Modelling Approach. Biological Invasions 4: 193–205. https://doi.org/10.1023/A:1020518915320

McKinney ML (2002) Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. Diversity and Distributions 8: 311–318. https://doi.org/10.1046/j.1472-4642.2002.00153.x

McNeill M, Payne T, Bewsell D (2008) Tourists as vectors of potential invasive alien species and a strategy to reduce risk. In: Fountain J, Moore K (Eds) Re-creating tourism: New Zealand Tourism and Hospitality Research Conference. Hanmer Springs (New Zealand), December 2008. Lincoln University, Canterbury, New Zealand, 3–5.

Overbeck GE, Vélez-Martin E, Scarano FR, Lewinsohn TM, Fonseca CR, Meyer ST, Müller SC, Ceotto P, Dadalt L, Durigan G, et al. (2015) Conservation in Brazil needs to include non-forest ecosystems. Diversity and Distributions 21: 1455–1460. https://doi.org/10.1111/ddi.12380

Pauchard A, García R, Zalba SM, Sarasola M, Zenni R, Ziller S, Nuñez MA (2015) 14 Pine Invasions in South America: Reducing Their Ecological Impacts Through Active Management. In: Canning-Clode J (Org.) Biological Invasions in Changing Ecosystems. 1ed. De Gruyter Open Ltd, Berlin.

Pickering C, Mount A (2010) Do tourists disperse weed seed? A global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. Journal of Sustainable Tourism 18: 239–256. http://dx.doi.org/10.1080/09669580903406613

Pretelli MG, Isacch JP, Cardoni DA (2015) Effects of fragmentation and landscape matrix on the nesting success of grassland birds in the Pampas grasslands of Argentina. Ibis 157, 688–699. https://doi.org/10.1111/ibi.12292

Pyšek P, Richardson DM (2010) Invasive Species, Environmental Change and Management, and Health. Annual Review of Environment and Resources 35: 25–55. http://dx.doi.org/10.1146/annurev-environ-033009-095548

Pyšek P, Jarošík V, Kučera T (2002) Patterns of invasion in temperate nature reserves. Biological Conservation 104: 13–24. https://doi.org/10.1016/S0006-3207(01)00150-1

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18: 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Radford IJ (2013) Fluctuating resources, disturbance and plant strategies: diverse mechanisms underlying plant invasions. Journal Arid Land 5(3): 284–297. https://doi.org/10.1007/s40333-013-0164-0

Randall RP (2017) A Global Compendium of Weeds. 3rd Edition. Randall RP, Perth, Australia, 1–3653.

Rew LJ, Fleming J (2011) Developing functional parameters for a science-based vehicle cleaning program to reduce transport of non-indigenous invasive plant species. Montana State Univ., Bozeman, 1–58. https://doi.org/10.21236/ADA553532

Ruiz GM, Carlton JT (2003) Invasion vectors: a conceptual framework for management. In: Ruiz G, Carlton J (Eds) Invasive species: Vectors and management strategies. Island Press,Washington, 459–504.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Säumel I, Kowarik I (2010) Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. Landscape and Urban Planning 94: 244–249. https://doi.org/10.1016/j.landurbplan.2009.10.009

Schrama M, Bardgett RD (2016) Grassland invasibility varies with drought effects on soil functioning. Journal of Ecology 104: 1250–1258. https://doi.org/10.1111/1365-2745.12606

Schüttler E, Karez CS (2008) Especies exóticas invasoras en las Reservas de Biosfera de América Latina y el Caribe. Un informe técnico para fomentar el intercambio de experiencias entre las Reservas de Biosfera y promover el manejo efectivo de las invasiones biológicas. Oficina Reg. Cienc. UNESCO para América Lat. El Caribe, Montevideo, 1–305.

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M et al. (2013) Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution 28: 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Taylor K, Brummer T, Taper ML, Wing A, Rew LJ (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity and Distributions 18: 942–951. https://doi.org/10.1111/j.1472-4642.2012.00926.x

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256–273. https://doi.org/10.1111/j.1469-8137.2007.02207.x

Veldman JW, Putz FE (2010) Long-distance Dispersal of Invasive Grasses by Logging Vehicles in a Tropical Dry Forest. Biotropica 42: 697–703. https://doi.org/10.1111/j.1744-7429.2010.00647.x

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Von Der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conservation Biology 21: 986–996. https://doi.org/10.1111/j.1523 1739.2007.00722.x

Von der Lippe M, Kowarik I (2008) Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients. Diversity and Distributions 14: 18–25. https://doi.org/10.1111/j.1472-4642.2007.00401.x

Ware C, Bergstrom DM, Müller E, Alsos IG (2012) Humans introduce viable seeds to the Arctic on footwear. Biological Invasions 14: 567–577. https://doi.org/10.1007/s10530-011-0098-4

Whinam J, Chilcott N, Bergstrom DM (2005) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. Biological Conservation 121: 207–219. https://doi.org/10.1016/j.biocon.2004.04.020

Wittenberg R, Cock MJW (2001) Invasive Alien Species: A Toolkit of Best Prevention and Management Practices. CAB International, Wallingford/Oxon, 1–228. https://doi.org/10.1079/9780851995694.0000

Zalba SM, Villamil CB (2002) Woody Plant Invasion in Relictual Grasslands. Biological Invasions 4: 55–72. https://doi.org/10.1023/A:1020532609792

Zalba S, Cuevas Y, De Villalobos A (2009) Lecciones aprendidas durante siete años de control de pinos invasores en pastizales naturales. In: Zalba S, Cuevas Y, De Villalobos A (Eds) Ambientes y recursos naturales del sudoeste bonaerense: producción, contaminación y conservación. EdiUNS, Bahia Blanca, Argentina, 325–340.

Ziller SR, Zalba S (2007) Proposals to prevent and control exotic invasive species. Natureza & Conservação 5: 78–85.

Zwaenepoel A, Roovers P, Hermy M (2006) Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic and Applied Ecology 1: 83–93. https://doi.org/10.1016/j.baae.2005.04.003

Appendix I

Potentially invasive species assessed. Species of invasive and potentially invasive alien plants present in intensive use zones of the Ernesto Tornquist Provincial Park and it's surroundings (Buenos Aires, Argentina)., potential impact (PIV), control difficulty (CDV), abundance, propagule production and proportion of months per year in which they are available for transport by each of the vectors identified in the area.

Species	Family	Category	PI	CD	Abundance	Propagule production	WIND	WILDLIFE	STREAMS	UNINTENTIONAL by people	INTENTIONAL by people	VEHICLES	CARGO
Acacia saligna	Fabaceae (Mimosoideae)	Invasive	Medium	High	Rare	High	0	0.25	0	0	1	0.25	1
Achillea milefollium	Asteraceae	Invasive	Medium	High	Rare	High	0.17	0	0	0	0	0.17	1
Aira elegantísima	Poaceae	Potentially Invasive	Medium	Low	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Argemone mexicana	Papaveraceae	Invasive	Medium	Medium	Rare	Moderate	0	0.17	0	0.25	0	0.25	1
Arundo donax	Poaceae	Invasive	Medium	High	Abundant	High	0	0	1	0	1	0	1
Bromus hordeaceus	Poaceae	Invasive	High	Medium	Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Buddleja davidii	Scrophulariaceae	Invasive	Medium	Medium	Abundant	Moderate	0.25	0	0	0	1	0.33	1
Carduus picnocephalus	Asteraceae	Potentially Invasive	High	Medium	Abundant	High	0.08	0	0	0.17	0	0.17	1
Carduus thoermeri	Asteraceae	Potentially Invasive	Medium	High	Very Abundant	High	0.08	0	0	0.17	0	0.17	1
Catapodium rigidum	Poaceae	Potentially Invasive	Medium	Low	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Chrysanthemum frutescens	Asteraceae	Invasive	Medium	High	Rare	Low	0.08	0	0	0	0	0.17	1
Convolvulus arvensis	Convolvulaceae	Invasive	Medium	High	Very Abundant	High	0	0	0	0	0	1	1
Cynodon dactylon	Poaceae	Invasive	High	High	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Cynosurus echinatus	Poaceae	Potentially Invasive	Medium	Low	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1

Species	Family	Category	PI	CD	Abundance	Propagule production	WIND	WILDLIFE	STREAMS	UNINTENTIONAL by people	INTENTIONAL by people	VEHICLES	CARGO
Datura ferox	Solanaceae	Invasive	Medium	High	Abundant	High	0	0.25	0	0	0	0.33	1
Digitaria sanguinalis	Poaceae	Potentially Invasive	Medium	Low	Abundant	High	0.08	0	0.08	0.17	0	0.17	1
Echinochloa crusgalli	Poaceae	Invasive	Medium	Medium	Very Abundant	Moderate	0.08	0	0.08	0.17	0	0.17	1
Eragrostis curvula	Poaceae	Potentially Invasive	High	High	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Eucalyptus globulus	Myrtaceae	Invasive	High	Medium	Abundant	High	0.25	0	0.25	0.33	1	0.33	1
Helianthus tuberosus	Asteraceae	Potentially Invasive	Low	Medium	Rare	Low	0.08	0	0	0.17	1	0.17	1
Ibicea lutea	Martyniaceae	Potentially Invasive	Medium	Medium	Rare	Low	0	0.17	0	0	1	0	1
Lantana montevidensis	Verbenaceae	Invasive	High	High	Abundant	Moderate	0	0.17	0	0	1	0.25	1
Ligustrum sinense	Oleaceae	Invasive	Medium	High	Very Abundant	High	0	0.17	0.17	0.25	1	0.25	1
Linaria texana	Scrophulariaceae	Potentially Invasive	Medium	Low	Rare	Low	0	0.08	0	0	1	0	1
Lolium multiflorum	Poaceae	Potentially Invasive	Medium	Medium	Very Abundant	Moderate	0.08	0	0	0.17	1	0.17	1
Lonicera japonica	Caprifoliaceae	Invasive	Medium	High	Abundant	Moderate	0	0.17	0	0.25	1	0.25	1
Lotus glaber	Fabaceae (Faboideae)	Potentially Invasive	Medium	High	Abundant	High	0	0	0	0.33	1	0.33	1
Matricaria recutita	Asteraceae	Potentially Invasive	Medium	Low	Very Abundant	Low	0.08	0	0	0.17	1	0.17	1
Melia azedarach	Meliaceae	Potentially Invasive	High	High	Rare	Very High	0	0.33	0	0.42	1	0.42	1
Melissa officinalis	Lamiaceae	Potentially Invasive	Low	Medium	Abundant	Low	0	0	0	0	1	0	1
Miriabilis jalapa	Nyctaginaceae	Invasive	High	High	Abundant	Moderate	0.17	0	0	0.25	1	0.25	1
Oenothera rosea	Onagraceae	Potentially Invasive	Low	Low	Rare	Low	0	0.17	0	0	1	0	1

Species	Family	Category	PI	CD	Abundance	Propagule production	WIND	WILDLIFE	STREAMS	UNINTENTIONAL by people	INTENTIONAL by people	VEHICLES	CARGO
Picris echiodes	Asteraceae	Potentially Invasive	Medium	Low	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Poa annua	Poaceae	Potentially Invasive	Medium	Medium	Very Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Polypogon monspeliensis	Poaceae	Potentially Invasive	Medium	Medium	Abundant	Moderate	0.08	0	0	0.17	0	0.17	1
Portulaca oleracea	Portulacaceae	Invasive	High	Medium	Very Abundant	High	0	0	0	0.25	1	0.25	1
Prunella vulgaris	Lamiaceae	Potentially Invasive	Medium	Low	Abundant	Low	0.17	0	0	0	1	0.25	1
Rapistrum rugosum	Brassicaceae	Potentially Invasive	Medium	Medium	Very Abundant	Moderate	0	0	0	0.25	0	0.25	1
Rhamnus alaternus	Rhamnaceae	Invasive	High	Medium	Very Abundant	High	0	0.25	0	0.33	0	0.33	1
Salix viminalis	Salicaceae	Potentially Invasive	Medium	Medium	Very Abundant	Moderate	0.17	0	1	0.25	1	0.25	1
Salsola kali	Quenopodiaceae	Invasive	High	High	Very Abundant	Moderate	0.17	0	0	0	0	0	1
Sisymbrium orientale	Brassicaceae	Potentially Invasive	Medium	Low	Very Abundant	Moderate	0	0	0	0.33	1	0.33	1
Solanum pseudocapsicum	Solanaceae	Potentially Invasive	High	Low	Abundant	Moderate	0	0.25	0	0	1	0.33	1
Tecoma stans	Bignoniaceae	Invasive	Medium	Medium	Rare	Moderate	0.08	0	0	0	0	0.17	1
Tradescanthia fluminensis	Commelinaceae	Invasive	Medium	Medium	Very Abundant	High	0	1	0	0	1	0	1
Ulex europeus	Fabaceae (Faboideae)	Potentially Invasive	High	High	Abundant	Moderate	0	0	0.25	0	0	0.33	1

Nature Conservation 24: 65–80 (2018)
doi: 10.3897/natureconservation.24.20019
http://natureconservation.pensoft.net

CONSERVATION IN PRACTICE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Cultural heritage and biodiversity conservation – plant introduction and practical restoration on ancient burial mounds

Orsolya Valkó[1], Katalin Tóth[2], András Kelemen[1,3], Tamás Miglécz[1,3], Szilvia Radócz[1], Judit Sonkoly[4], Béla Tóthmérész[1,2], Péter Török[4], Balázs Deák[2]

1 *University of Debrecen, Department of Ecology, Debrecen, Egyetem tér 1, H-4032 Hungary* **2** *MTA-DE Biodiversity and Ecosystem Services Research Group, Debrecen, Egyetem tér 1, H-4032 Hungary* **3** *MTA's Post Doctoral Research Programme, MTA TKI, Nádor utca 7, Budapest, H-1051 Hungary* **4** *MTA-DE Lendület Functional and Restoration Ecology Research Group, Egyetem tér 1, Debrecen, H-4032, Hungary*

Corresponding author: *Orsolya Valkó* (valkoorsi@gmail.com)

Academic editor: *S. Lengyel* | Received 03 August 2017 | Accepted 18 December 2017 | Published 5 January 2018

http://zoobank.org/86E45E91-57B7-44EB-A1E5-ED9F26C73A43

Citation: Valkó O, Tóth K, Kelemen A, Miglécz T, Radócz S, Sonkoly J, Tóthmérész B, Török P, Deák B (2018) Cultural heritage and biodiversity conservation – plant introduction and practical restoration on ancient burial mounds. Nature Conservation 24: 65–80. https://doi.org/10.3897/natureconservation.24.20019

Abstract

Linking the conservation of cultural heritage and natural values provides a unique opportunity for preserving traditional landscapes and receives an increased awareness from stakeholders and society. Ancient burial mounds are proper objects of such projects as they are iconic landscape elements of the Eurasian steppes and often act as refugia for grassland specialist species. The aim of this project was to reintroduce grassland plant species to burial mounds for representing them as cultural monuments with the associated biodiversity for the public. The effectiveness of seed sowing, transplanting greenhouse-grown plants and individuals from threatened populations on burial mounds in Hortobágy National Park, Hungary was tested. The following questions were answered: (1) which method is the most effective for species introduction? (2) which species can establish most successfully? (3) how does management affect the species establishment rates? It was found advisable to use a combination of seed sowing and transplanting greenhouse-grown plants. Sowing was found as a cost-effective method for introducing large-seeded species, whilst introduction of greenhouse-grown transplants warranted higher establishment rates for a larger set of species. Transplanting adult individuals was more reliable regardless of management regimes, however this method is labour-intensive and expensive. Intensive management, like mowing with heavy machinery and intensive grazing, should be avoided in the first few years after introduction. The authors highlighted the fact that introducing characteristic grassland species on cultural monuments offers a great opportunity to link issues of landscape and biodiversity conservation. This project demonstrated that, by the revitalisation of cultural monuments, cultural ecosystem services can also be restored.

Keywords

cultural ecosystem services; endangered species; grassland restoration; landscape conservation; landscape element; reintroduction

Introduction

Open landscapes often harbour surprisingly high biodiversity and they are also an essential part of our cultural heritage (Dengler et al. 2014). The European Landscape Convention was initiated to protect and sustain European landscapes characteristic of certain countries and cultures (Jones 2007). Protection of the traditional landscape structure and land use types can considerably contribute to biodiversity conservation by ensuring the optimum landscape configuration and proper management for semi-natural habitats (Babai and Molnár 2014, Plieninger et al. 2015, Szilassi et al. 2017). One of the major threats to European landscapes is the huge loss of habitats due to the intensive land use of past centuries (Lindborg et al. 2015, Hüse et al. 2016). In the near future, increasing demands for natural resources are expected to further accelerate the rate of habitat degradation and species extinctions (Guerrant et al. 2004). Since grasslands harbour an extraordinarily high diversity, their conservation and restoration are high-priority tasks (Valkó et al. 2016a).

Integrating cultural ecosystem services into landscape planning and protection can effectively support nature conservation projects which aim to conserve historical landscape elements with a potential of harbouring high biodiversity and providing ecosystem services (Jones et al. 2016, Ramos et al. 2016). Ancient burial mounds called ‘kurgans’ can serve as ideal objects for such projects. Kurgans are earthen burial mounds built by nomadic tribes from the Late Copper Age to the medieval period (Sudnik-Wójcikowska et al. 2011, Bede et al. 2015). They are iconic landscape elements of the Eurasian steppes and have a considerable role in the life of local people as historical and sacred places (Deák et al. 2016a, Sudnik-Wójcikowska et al. 2011). Their size ranges from a few hundred square metres to one hectare and their height is usually between 1 and 15 metres (Deák et al. 2016a). Their special shape makes them prominent landscape elements in plain areas. The estimated number of kurgans is 400–600,000 in the steppe region (Deák et al. 2016a), thus they can be considered as typical elements of the steppe biome.

Besides their cultural and aesthetic value, burial mounds often act as biodiversity hotspots in agricultural landscapes. Their particular shape and steep slopes have often prevented ploughing; thus, grassland vegetation has been able to survive on burial mounds (Deák et al. 2016b, Dembicz et al. 2016). This is especially true for loess grasslands which are often restricted to burial mounds and road verges in many regions

(Sudnik-Wójcikowska et al. 2011, Deák et al. 2016a, b). Given the importance of burial mounds in landscape protection and biodiversity conservation, they can serve as representative spots for the demonstration of the results of conservation projects. Their importance is acknowledged by the European Landscape Convention and they are considered typical landscape elements of Hungary (Jones 2007, Jones et al. 2016). Despite their legal protection, urbanisation and ploughing considerably threaten the vegetation of the burial mounds, thus in many cases active restoration measures are needed for their revitalisation (Deák et al. 2016a). Due to the scattered distribution and relatively small area of the burial mounds, small-scale and volunteer NGO projects can contribute considerably to preserving or restoring their biodiversity.

Spontaneous recovery of target plant populations in degraded landscapes is often hampered by propagule-limitation, i.e. the lack of target species in the seed banks and seed rain, as many grassland plant species have transient seed banks and many are dispersal-limited (Baur 2014). Thus, active management strategies such as reintroduction of plant populations to appropriate habitats have become increasingly integrated into conservation practice (Maunder 1992, Rout et al. 2009). However, in spite of this huge number of species introduction projects and the urgent need for best practices from the practitioner's side, there are only a few available studies in this topic (Bottin et al. 2007, Godefroid et al. 2011a). A search for scientific articles in the ISI Web of Knowledge using the keywords "plant species introduction" and "conservation" confined to the countries of the European Union, returned only 183 hits. These hits were screened by title and only 21 publications were found that concerned plant species introduction projects. Information is especially lacking about negative results and failures, however these can be highly informative for practitioners in order to avoid future problems (Godefroid et al. 2011b). Latter cases are of high importance as most of the species introduction projects are not considered as comprehensively successful, thus information about potential problems would be especially helpful in planning such projects (Allen 1994).

The authors introduced historically widespread species of loess grasslands on burial mounds with species-poor and degraded vegetation in the Hortobágy National Park, Hungary. An approach which was found to be effective in restored grasslands was used, i.e. creating establishment hot-spots for grassland specialist plant species (see also Valkó et al. 2016b), from where they are able to colonise the whole habitat patch. The overall aim was to introduce typical grassland species to create representative sites demonstrating burial mounds as landscape elements with the associated biodiversity for the public. Three methods were used for species introduction: seed sowing, planting individuals grown in greenhouses and translocating adult plants from threatened natural populations, which otherwise would probably become extinct. As it was primarily a conservation-focused and not a scientific project, species lists, sowing densities and the number of introduced individuals were determined according to the demands of the site manager. Due to the abovementioned reasons, it was not possible to run state-of-the-art statistical analyses which should be considered during the interpretation of the results. However publication of the authors' experiences was considered of a high importance, as Godefroid et al. (2011b) also pointed out, a major problem is that in many cases results of non-scientific plant reintroduction projects remain in unpublished internal reports. The following questions were asked: (1) which method is the most effective for species introduction? (2) which species can establish most successfully? (3) how does management affect the establishment rate and flowering success of the target species?

Materials and methods

Study sites

The study sites are situated in the Great Hungarian Plain, in the Hortobágy National Park (N47.58°, E20.92°). The climate of the area is moderately continental with a mean annual temperature of 9.5 °C and mean annual precipitation of 550 mm (Lukács et al. 2015). The National Park is a UNESCO World Heritage site, due to the large areas of connected open landscapes and the associated traditional pastoral practices. Typically, burial mounds are covered by loess grassland vegetation (*Festucion rupicolae;* Deák et al. 2014). Due to their fertile chernozem soils, the majority of loess grasslands have been converted into arable fields in the region. They have mostly been preserved on sites unsuitable for arable farming, for example, on burial mounds.

Target species were reintroduced on to five burial mounds (see Table 1). All burial mounds harboured degraded and generally species-poor loess grasslands, characterised by grasses such as *Festuca rupicola*, *Poa angustifolia* and *Bromus inermis*. Several weedy species with good competitor abilities, which are unwanted from a nature conservation viewpoint, were present in the vegetation (*Bromus sterilis*, *Carduus acanthoides*, *Cirsium arvense*, *Lycium barbarum* and *Elymus repens*) and target forb species of loess grasslands were lacking. Two burial mounds with the steepest slopes (Filagória and Meggyes) were managed by the authors; they mowed the kurgans by a hand-held mowing machine three times a year (late April, mid-June and late August, every year from 2010 to 2015) and removed the hay by raking (Supplementary material 1). Two burial mounds with more gentle slopes (Nyíregyházi and Porosállás) were mown by heavy machinery, once a year

Table 1. Site characteristics of the studied kurgans.

	Filagória	Meggyes	Görbeszék	Nyíregyházi	Porosállás
Coordinates	N47.573271°, E20.942839°	N47.585222°, E20.973992°	N47.589589°, E20.872901°	N47.570090°, E20.951617°	N47.550524°, E20.881466°
Total area (m^2)	7500	4500	1600	10000	17000
Height (m)	7	2	8	5.5	2.5
Total vegetation cover (%)	78.0±10.4	84.0±6.6	77.0±5.8	78.0±5.7	87.0±5.7
Vegetation height (cm)	67.0±20.8	83.0±17.5	36.0±9.6	62.0±17.9	72.0±14.8
Management type	mown (hand)	mown (hand)	grazed (sheep)	mown (machinery)	mown (machinery)

in mid-June and the hay was removed by machinery. One burial mound (Görbeszék) was managed by extensive grazing by sheep; the grazing intensity was approximately 0.8 animal unit/ha. The grazing season lasted from late April to mid-October. The area which was affected by species reintroduction was approximately 0.25 ha in the studied kurgans.

Plant introduction

The aim of the project was to reintroduce characteristic loess grassland species to the studied burial mounds. Experts of the Hortobágy National Park Directorate selected the list of introduced species and also recommended the set of species to be reintroduced to certain kurgans. They selected a total of 18 species typical of the loess grasslands of the region. Three measures were applied for plant reintroduction: seed sowing, planting of individuals grown in the greenhouse (transplantation) and planting adult plants from threatened natural populations (translocation).

Seed collection

At the first stage of plant introduction, seeds of 16 target species were collected in 2013. Seeds originated from semi-natural loess grasslands of the region. The authors could not collect seeds of two endangered species (*Amygdalus nana* and *Anchusa barrelieri*), as from their few existing scattered populations, it was impossible to collect ripened viable seeds. For *Rosa rubiginosa*, seeds were collected before maturation (in late September) because, in that season, the amount of germination inhibitor compounds is lower in the pericarp (Haouala et al. 2013). The collected seed material was the basis for seed sowing (15 species) and also for growing individuals in a greenhouse (11 species). Germination tests were performed for all species; the germination rates of three sorts of 100 seeds per each species (altogether 300 seeds) were monitored from October 2013 to June 2014 (altogether 36 weeks).

Seed sowing

The collected seeds of herbaceous species were sown, after soil disturbance by raking in October 2013 (see Table 2). Scarification or stratification was not applied on the seeds of herbaceous species. Three characteristic species of loess grasslands (*Filipendula vulgaris*, *Salvia austriaca* and *S. nemorosa*) were sown as matrix forb (amount of 500 g seeds per burial mound). Other species were sown in an amount of 20 g seeds per burial mound.

Transplantation

Using the collected seed material, individuals of 11 target species were grown in a greenhouse (see Table 2). The seeds were sown in pots in March 2014. The only exception was *Rosa rubiginosa* which was sown in November 2013 and was grown under outdoor conditions because cold stratification has proved to be an effective method for breaking the seed dormancy of rose species (Zhou and Bao 2011). Germinated plants

Table 2. List of species introduced on the five kurgans. (A) Sown species and the amount of sown seeds (g), (B) Species list and number of greenhouse-grown transplants and (C) Species list and number of individuals translocated from threatened natural populations. Matrix species are marked with an asterisk.

	Filagória	Görbeszék	Meggyes	Nyíregyházi	Porosállás
(A) Seed sowing					
Carthamus lanatus		20 g	20 g		
Centaurea pannonica	20 g		20 g	20 g	20 g
Centaurea sadleriana	20 g	20 g		20 g	
Centaurea solstitialis	20 g		20 g		
Dianthus pontederae	20 g		20 g	20 g	20 g
*Filipendula vulgaris**	500 g		500 g	500 g	500 g
Galium verum	20 g				
Hypericum perforatum	20 g				
Knautia arvensis	20 g				
Lotus corniculatus					20 g
Lycopsis arvensis			20 g		
Phlomis tuberosa	20 g	20 g	20 g	20 g	20 g
*Salvia austriaca**	500 g		500 g	500 g	500 g
*Salvia nemorosa**	500 g		500 g	500 g	500 g
Silene vulgaris	20 g		20 g	20 g	
(B) Transplantation					
Carthamus lanatus		30			
Centaurea pannonica	38		30		
Centaurea sadleriana	50	45		50	
Centaurea solstitialis					
Dianthus pontederae	20		20	30	50
Filipendula vulgaris	20		20	30	50
Lotus corniculatus					34
Rosa rubiginosa	49				
Salvia austriaca			10	20	50
Salvia nemorosa	30		10	20	50
Silene vulgaris	36		20		
(C) Translocation					
Amygdalus nana	35			25	
Anchusa barrelieri				32	
Phlomis tuberosa	32	124	10	53	20

were transplanted to the kurgans in early September 2014. All transplants were marked with sticks and were watered for one week after transplanting to facilitate rooting and acclimatisation. The average temperature of the region was 17.3°C, and there was 54 mm precipitation in that month (HCSO 2017). In November 2014, mulching (using an approximately 0.5 cm thick layer of hay) was applied at the basal parts of the stems in order to prevent freezing.

Translocation

In the case of three endangered species, adult plants were translocated to the kurgans from endangered natural populations in the region (Table 2). The individuals of *Amygdalus nana* and *Phlomis tuberosa* were translocated from populations situated in road verges which were threatened both by intensive mowing and herbicide application. The individuals of *Anchusa barrelieri* originated from the margin of an arable field and were threatened by ploughing and fertiliser run off. Individuals were translocated in September 2013. All translocated individuals were marked with sticks and were treated similarly (watering and mulching) to the greenhouse grown transplants (Supplementary material 1).

Sampling of introduction success

The survival rate of introduced species was tested in September 2015 by counting all individuals. To evaluate reproductive success, the species which flowered or set seeds in September 2015 were listed. For sown species, the establishment rates were calculated as follows. From germination rates in the greenhouse experiment, the predicted numbers of individuals were calculated on the burial mounds using the following equation: $N_p = SN_s \times (N_g/100)$, where N_p is the predicted number of individuals per burial mound; SN_s is the number of seeds sown on burial mounds and N_g is the number of germinated individuals in the greenhouse experiment. The observed number of individuals were compared with the predicted numbers of individuals. For transplanted and translocated species, the establishment rate was calculated as the ratio of planted individuals/surviving individuals.

Results

The results of the germination experiment showed that the majority of species had good germination rates under greenhouse conditions, regardless of their thousand-seed weights (Supplementary material 1). The observed establishment rates of sown species on the burial mounds were lower than the predicted values (a mean of 0.55 % ± 2.57 SD; Table 3). The establishment rate of sown species was the highest on the two burial mounds (Filagória and Meggyes) which were managed by hand mowing (Table 3). Only two sown species (*Carthamus lanatus* and *Lycopsis arvensis*) had an establishment rate higher than 10% on at least one burial mound. These two species were those with the highest thousand-seed weights (Supplementary material 1). There were six species (*Centaurea pannonica*, *C. sadleriana*, *Dianthus pontederae*, *Filipendula vulgaris*, *Lotus corniculatus* and *Phlomis tuberosa*) which failed to establish on any of the burial mounds after seed sowing (Table 3).

The establishment rate of transplanted plants was the highest on the two burial mounds (Filagória and Meggyes) which were managed by hand mowing (Table 3). The highest establishment rates were detected for *Rosa rubiginosa*, *Salvia austriaca* and *S. nemorosa*. There were three species (*Carthamus lanatus*, *Dianthus pontederae* and *Lotus corniculatus*) which failed to establish on any of the burial mounds.

Table 3. Establishment rates in September 2015 (%) of (A) sown species, (B) greenhouse-grown transplants and (C) individuals translocated from threatened natural populations. Species which had flowering individuals are marked with an asterisk.

	Filagória	Görbeszék	Meggyes	Nyíregyházi	Porosállás
(A) Seed sowing					
Carthamus lanatus		0.00	12.61*		
Centaurea pannonica	0.00		0.00	0.00	0.00
Centaurea sadleriana	0.00	0.00		0.00	
Centaurea solstitialis	0.11*		0.75*		
Dianthus pontederae	0.00		0.00	0.00	0.00
Filipendula vulgaris	0.00		0.00	0.00	0.00
Galium verum	0.08*				
Hypericum perforatum	0.02*				
Knautia arvensis	0.24*				
Lotus corniculatus					0.00
Lycopsis arvensis			10.68*		
Phlomis tuberosa	0.00	0.00	0.00	0.00	0.00
Salvia austriaca	0.51*		0.03*	0.00	0.01
Salvia nemorosa	0.37*		0.33*	0.01	0.02
Silene vulgaris	0.03*		0.00	0.00	
(B) Transplantation					
Carthamus lanatus		0.00			
Centaurea pannonica	10.50*		3.30*		
Centaurea sadleriana	8.00	51.10*		0.00	
Dianthus pontederae	0.00		0.00	0.00	0.00
Filipendula vulgaris	10.00		0.00	0.00	0.00
Lotus corniculatus					0.00
Rosa rubiginosa	75.50				
Salvia austriaca			60.00*	5.00	6.00
Salvia nemorosa	100.00*		90.00*	10.00*	36.00*
Silene vulgaris	5.60*		0.00		
(C) Translocation					
Amygdalus nana	37.10			0.00	
Anchusa barrelieri				56.30*	
Phlomis tuberosa		66.10*		75.50*	75.00*

Establishment rates of individuals translocated from threatened natural populations were higher than 50% on all sites for *Anchusa barrelieri* and *Phlomis tuberosa* (Table 3). The establishment rate of *Amygdalus nana* was 37.1 % on Filagória kurgan, managed by hand-mowing. The species failed to establish on Nyíregyházi kurgan, which was managed by mowing machinery.

Altogether, 12 species having individuals with flowering shoots were found. The highest proportion of flowering species was found on burial mounds managed by hand mowing (Filagória and Meggyes). Of the established species, *Amygdalus nana*, *Filipendula vulgaris* and *Rosa rubiginosa* failed to flower on any of the kurgans.

Discussion

The study demonstrated that all three methods (seed sowing, transplanting and translocating) were feasible for plant introduction. Based on these results, several circumstances, such as site conditions, management type, species characteristics, available manpower and financial limitations should be considered when choosing the most feasible method.

Seed sowing

Sowing the seeds of target species is considered to be the least labour- and cost-intensive method for species introductions (Guerrant and Kaye 2007). However, this study and several other papers reported that seed sowing has the lowest success rate amongst the widely applied plant introduction methods, because seed germination in the field is influenced by many factors and is often rather unpredictable (Menges 2008, Becker 2010). It was found that the success of seed sowing largely depended on specific germination features, management and local environmental conditions. Besides these factors, the introduction success also depends on the timespan of the monitoring. For instance, several seeds, especially those with a hard seed coat, germinate after several years of dormancy in natural conditions (Baskin and Baskin 1998). Thus, these seeds might be able to germinate in the future years.

The quality of the collected seed material was assessed by the germination success of all target plant species from which viable seeds could be collected. It was found that the seeds of all collected species germinated under greenhouse conditions, however, species with a hard seed coat (*Lotus corniculatus*, *Lycopsis arvensis*, *Phlomis tuberosa* and *Salvia austriaca*) and most species of the family *Asteraceae* (*Carthamus lanatus*, *Centaurea pannonica* and *C. sadleriana*) had moderate germination rates in the greenhouse. On the one hand, as many of these species require some mechanism to break seed dormancy (Baskin and Baskin 1998), in future projects, testing scarification or stratification measures on such seeds is recommended in order to increase their establishment success. On the other hand, seed predator insects often consume the seeds of these species (Steffan-Dewenter et al. 2001) and, even though the seed material of infested seeds was carefully cleaned, some of them remained in the seed material.

It was found that species with high thousand-seed weights (especially *Carthamus lanatus* and *Lycopsis arvensis*) could establish most successfully on the burial mounds. It was also found in former studies that species with large seeds can better tolerate the shading effect of litter and can also germinate below thick litter layers (Miglécz et al. 2013). Litter accumulation is typical in the loess grasslands of the region; Kelemen et al. (2013) reported amounts of litter ranging between 161–516 g/m^2. This suggests that large-seeded species can have an establishment advantage compared to small-seeded ones under such conditions (see also Ambika et al. 2014). Therefore, sowing species with large seeds is advisable in such projects and, by the application of these species, the cost efficiency of the project can be increased.

In many cases, seeds failed to germinate due to the lack of proper establishment microsites (see also Deák et al. 2011). It was found that seed sowing was most effective on burial mounds which were managed by hand mowing. Hand mowing usually creates a higher diversity of microsites favourable for plant germination compared to the homogeneous vegetation structure formed by mowing machinery (Humbert et al. 2009). In the study sites, hand mowing was performed three times a year, which supported higher vegetation openness compared to kurgans mown once a year by machinery. More frequent hand mowing was likely to be more effective in weed control than less frequent mowing by machinery and, at the early mowing dates, weeds could be removed before their seeds ripened (Kelemen et al. 2014). By hand mowing, it was also possible to give an advantage to introduced species by avoiding cutting them before seed ripening. Grazing is usually associated with a higher trampling disturbance than hand mowing (Tälle et al. 2016, Tóth et al. 2016) resulting in the failure of germination of the sown species on the grazed Görbeszék kurgan. Based on these findings, for the effective introduction of target species by seed sowing, either hand mowing or soil preparation by raking or smooth harrowing is necessary (Klaus et al. 2017, Valkó et al. 2016b). Higher flowering ratio of introduced species on hand mown sites compared to the sites mown by machinery also shows the advantages of hand mowing versus mowing by machinery.

Even though seed sowing is considerably less labour-intensive than the transplanting of individuals, important drawbacks of the method were identified. The success of seed sowing largely depends on the germination rates of the available seed material (see also Godefroid et al. 2011a). In many cases, it is difficult to harvest viable seeds from certain species, especially from rare ones (such as *Anchusa barrelieri* and *Amygdalus nana* in this study). This is due to the fact that they usually have small and scattered populations and often one of the reasons for their vulnerability is the low seed production itself (Bottin et al. 2007). Thus, seed sowing cannot be an option for the reintroduction of species with low availability of ripened seeds or very low germination rates. Given the abovementioned drawbacks, seed sowing can be recommended only in certain cases. It can be a feasible option in the case of large-seeded species, which can tolerate litter accumulation, or on sites where the availability of establishment microsites is high, but the intensity of trampling and biomass removal is moderate.

Transplanting and translocation

Both transplanting of juvenile and adult plants proved to be a more effective method than seed sowing, as individuals are introduced at a more developed ontogenetic stage which increases the probability of successful establishment (Guerrant and Kaye 2007, Wallin et al. 2009). However, it should be considered that, even though transplantation and translocation were successful in the first year, dynamics might be different in following years. Even though transplanting adult individuals is considerably more labour-intensive and expensive than seed sowing, this method was more reliable and less sensitive to site characteristics and management regimes. The most successful establishment was found in the case of species with well-developed root systems or belowground storage organs, such as *Salvia austriaca*, *S. nemorosa*, *Phlomis tuberosa, Amygdalus nana* and *Anchusa barrelieri* (Kutschera et al. 1992).

By translocation, individuals of the threatened donor populations could be saved. All three species which were translocated from threatened natural populations established successfully and two of them (*Anchusa barrelieri* and *Phlomis tuberosa*) had flowering and fruiting individuals on the burial mounds and were thus able to establish a new population on the recipient site. This result indicates the importance of this kind of conservation action which aims to translocate individuals from threatened populations to suitable habitats.

Plants are in a sensitive period for a few months after transplantation and translocation; thus, in this early period, intense disturbance, such as trampling, mowing or grazing should be avoided (Bottin et al. 2007). Besides, transplantation and translocation themselves are often associated with small-scale soil disturbance and these disturbed soil surfaces can be starting points for weed encroachment (Török et al. 2012). As mowing and grazing are not feasible management options in the very close vicinity of recently planted individuals, weeds growing close to the planted plants were suppressed by cutting them with pruning shears.

Implications for nature conservation

Based on these results, in plant introduction projects, it is crucial to collect basic seed material from a local provenance and to test the germination ability of seeds. One part of the seeds can be used for seed sowing on the field and the other part should be germinated in a greenhouse. In the case of larger seeded species, greater success with seed sowing than in the case of smaller-seeded ones can be expected. With transplanting and translocating individuals, the establishment success can be increased, but it is crucial to ensure proper water availability and protect the transplants from severe disturbance.

Godefroid et al. (2011a, b) pointed out that there is a considerable publication bias in plant introduction studies: usually only the successful results are published. Experiences of failures or problems generally remain unavailable to the public, even though they would be very useful for planning and implementing plant introduction projects. In this case, most of the difficulties were associated with improper management (use of mowing machinery) or too intense competition by neighbouring vegetation (see also Kelemen et al. 2015). These results suggest that post-introduction management is a crucial factor which has to be carefully planned and implemented in future projects. In the first year after introduction, mowing by machinery or grazing should be avoided, as these management types are associated with too intense non-selective trampling and biomass removal. Mowing by hand proved to be the best management option in the first few years, because in this way, the mowing of young transplanted individuals which are at a life stage highly sensitive to disturbance could be avoided. Later on, both grazing and mowing can be viable management options, depending on site characteristics, grassland type and available resources (Tälle et al. 2016).

This study demonstrated that landscape and biodiversity conservation can be linked by species reintroduction projects in historical landscapes. For such projects, burial mounds are ideal objects because they can act as representative spots for society.

These results draw attention to the necessity of restoring the landscape and biodiversity values of kurgans which are important parts of the cultural heritage across Eurasia. The need to link conservation and introduction programmes on cultural monuments should be emphasised.

To support future plant reintroduction projects, the following findings should be considered:

Seed material should be collected from regional populations to ensure the use of locally adapted ecotypes. Before large-scale application, indoor germination tests are recommended.

The use of a combination of seed sowing and transplanting greenhouse-grown plants is advisable. Seed sowing is a cost-effective method for introducing large-seeded species, whilst introduction of greenhouse-grown transplants warrants higher establishment rates for a larger set of species.

To create proper microsites for germination and establishment, it is crucial to lightly disturb the soil surface by raking prior to seed sowing.

As post-introduction management, regular watering and mulching is necessary to prevent drought, freezing and weed invasion after transplanting.

Intensive management, such as mowing with heavy machinery and intensive grazing, should be avoided in the first few years after introduction.

This project demonstrated that by the revitalisation of cultural ecosystem services, such as aesthetic values, public relations and educational values, can be restored at the same time (Plieninger et al. 2013). During the project, several layers of society could be involved. Several volunteers participated in the re-introduction and post-management actions. Due to the increased public awareness, the restored kurgans became part of the public demonstration route system in the Hortobágy National Park. By demonstrating the natural and cultural values of these cultural monuments, a wider society will become familiar with the historical, natural and landscape values of these monuments. Two of the restored kurgans became involved in the field courses of Hungarian and foreign institutes of higher education, representing the technical details of plant re-introduction and their nature conservation advances. In a few years, it will be possible to re-introduce moderate grazing, which is the traditional land use in the area and which is beneficial for local farmers, who can make use of the area.

Acknowledgements

We are grateful to E. Tóth, L. Gál, K. Süveges and Á. Lovas-Kiss for their help in the seed collection, soil preparation and transplantation. We are grateful to T. Hartel, A. Helm and S. Lengyel for their constructive comments on the manuscript. The restoration project was funded by the Hortobágy National Park and the KEOP-3.1.2/2F/09-11-2011-0009 project. The study was supported by OTKA PD 111807

(OV), NKFI FK 124404 (OV), NKFI KH 126476 (OV), NKFI KH 126477 (BT), OTKA PD 115627 (BD), OTKA K 116639 (BT), NKFI PD 124548 (TM) and NKFIH K 119225 (PT) projects. OV and BD were supported by the Bolyai János Research Scholarship of the Hungarian Academy of Sciences. Authors were funded by the MTA's Post Doctoral Research Programme. OV and BD were supported by the ÚNKP-17-4-III-DE-151 and ÚNKP-17-4-III-DE-160 New National Excellence Programme of the Ministry of Human Capacities. We are grateful to L. Papp and the Botanical Garden of the University of Debrecen for their support in the greenhouse experiments.

References

Allen WH (1994) Reintroduction of endangered plants. Bioscience 44: 65–68. https://doi.org/10.2307/1312203

Ambika S, Manonmani V, Somasundaram G (2014) Review on effect of seed size on seedling vigour and seed yield. Research Journal of Seed Science 7: 31–38. https://doi.org/10.3923/rjss.2014.31.38

Babai D, Molnár Z (2014) Small-scale traditional management of highly species-rich grasslands in the Carpathians. Agriculture, Ecosystems & Environment 182: 123–130. https://doi.org/10.1016/j.agee.2013.08.018

Baskin CC, Baskin JM (1998) Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Elsevier.

Baur B (2014) Dispersal-limited species – A challenge for ecological restoration. Basic and Applied Ecology 15: 559–564. https://doi.org/10.1016/j.baae.2014.06.004

Becker T (2010) Explaining rarity of the dry grassland perennial *Astragalus exscapus*. Folia Geobot 45: 303–321. https://doi.org/10.1007/s12224-010-9068-3

Bede Á, Salisbury RB, Csathó AI, Czukor P, Páll DG, Szilágyi G, Sümegi P (2015) Report of the complex geoarcheological survey at the Ecse-halom kurgan in Hortobágy, Hungary. Central European Geology 58: 268–289. https://doi.org/10.1556/24.58.2015.3.5

Bottin L, Le Cadre S, Quilichini A, Bardin P, Moret J, Machon N (2007) Re-establishment trials in endangered plants: a review and the example of *Arenaria grandiflora*, a species on the brink of extinction in the Parisian region (France). Ecoscience 14: 410–419. https://doi.org/10.2980/1195-6860(2007)14[410:RTIEPA]2.0.CO;2

Deák B, Tóthmérész B, Valkó O, Sudnik-Wójcikowska B, Bragina TM, Moysiyenko I, Apostolova I, Bykov N, Dembicz I, Török P (2016a) Cultural monuments and nature conservation: The role of kurgans in maintaining steppe vegetation. Biodiversity and Conservation 25: 2473–2490. https://doi.org/10.1007/s10531-016-1081-2

Deák B, Valkó O, Török P, Tóthmérész B (2016b) Factors threatening grassland specialist plants – A multi-proxy study on the vegetation of isolated grasslands. Biological Conservation 204: 255–262. https://doi.org/10.1016/j.biocon.2016.10.023

Deák B, Valkó O, Alexander C, Mücke W, Kania A, Tamás J, Heilmeier H (2014) Fine-scale vertical position as an indicator of vegetation in alkali grasslands – Case study based on remotely sensed data. Flora 209: 693–697. https://doi.org/10.1016/j.flora.2014.09.005

Dembicz I, Moysiyenko II, Shaposhnikova A, Vynokurov D, Kozub L, Sudnik-Wójcikowska B (2016) Influence of isolation and size of a habitat patch on plant species density on kurgans and within other refuges of Ukrainian steppe. Biodiversity and Conservation 25: 2289–2307. https://doi.org/10.1007/s10531-016-1077-y

Dengler J, Janišová M, Török P, Wellstein C (2014) Biodiversity of Palaearctic grasslands: A synthesis. Agriculture, Ecosystems & Environment 182: 1–14. https://doi.org/10.1016/j.agee.2013.12.015

Godefroid S, Piazza C, Rossi G, Buord S, Stevens A-D, Aguraiuja R, Cowell C, Weekly CW, Vogg G, Iriondo JM, Johnson I, Dixon B, Gordon D, Magnanon S, Valentin B, Bjuerke K, Koopman R, Vincens M, Virevaire M, Vanderborgth TS (2011a) How successful are plant species reintroductions? Biological Conservation 144: 672–682. https://doi.org/10.1016/j.biocon.2010.10.003

Godefroid S, Vanderborght T (2011b) Plant reintroductions: The need for a global database. Biodiversity and Conservation 20: 3683–3688. https://doi.org/10.1007/s10531-011-0120-2

Guerrant EO, Kaye TN (2007) Reintroduction of rare and endangered plants: common factors, questions and approaches. Australian Journal of Botany 55: 362–370. https://doi.org/10.1071/BT06033

Guerrant EO, Havens K, Maunder M (2004) Ex situ Plant Conservation: Supporting Species Survival in the Wild. Island Press, Washington.

Haouala F, Hajlaoui N, Cheikh-Affene Z-B (2013) Enhancing seed germination in rose (*Rosa rubiginosa* L.). Medicinal & Aromatic Plants 2: 139. https://doi.org/10.4172/2167-0412.1000139

Humbert J-Y, Ghazoul J, Walter T (2009) Meadow harvesting techniques and their impacts on field fauna. Agriculture, Ecosystems & Environment 130: 1–8. https://doi.org/10.1016/j.agee.2008.11.014

Hungarian Central Statistical Office (2017) Hungarian Central Statistical Office. http://www.ksh.hu/docs/hun/xstadat/xstadat_evkozi/e_met002.html

Hüse B, Szabó S, Deák B, Tóthmérész B (2016) Mapping ecological network of green habitat patches and their role in maintaining urban biodiversity in and around Debrecen city (Eastern Hungary). Land Use Policy 57: 574–581. https://doi.org/10.1016/j.landusepol.2016.06.026

Jones M (2007) The European Landscape Convention and the question of public participation. Landscape Research 32: 613–633. https://doi.org/10.1080/01426390701552753

Jones PJ, Andersen E, Capitani C, Carvalho Ribeiro S, Griffiths GH, Loupa-Ramos I, Madeira L, Mortimer SR, Paracchini ML, Pinto Correia T, Schmidt AM, Simoncini R, Wascher DM (2016) The EU societal awareness of landscape indicator: A review of its meaning, utility and performance across different scales. Land Use Policy 53: 112–122. https://doi.org/10.1016/j.landusepol.2015.01.038

Kelemen A, Lazzaro L, Besnyői V, Albert Á-J, Konečná M, Dobay G, Memelink I, Adamec V, Götzenberger L, de Bello F, Le Bagousse-Pinguet Y, Lepš J (2015) Net outcome of competition and facilitation in a wet meadow changes with plant's life stage and community productivity. Preslia 87(4): 347–361.

Kelemen A, Török P, Valkó O, Deák B, Miglécz T, Tóth K, Ölvedi T, Tóthmérész B (2014) Sustaining recovered grasslands is not likely without proper management: vegetation changes and large-scale evidences after cessation of mowing. Biodiversity and Conservation 23: 741–751. https://doi.org/10.1007/s10531-014-0631-8

Kelemen A, Török P, Valkó O, Miglécz T, Tóthmérész B (2013) Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. Journal of Vegetation Science 24: 1195–1203. https://doi.org/10.1111/jvs.12027

Klaus V, Schäfer D, Kleinebecker T, Fischer M, Prati D, Hölzel N (2017) Enriching plant diversity in grasslands by large-scale experimental sward disturbance and seed addition along gradients of land-use intensity. Journal of Plant Ecologyogy 10: 581–591. https://doi.org/10.1093/jpe/rtw062

Kutschera L, Lichtenegger E, Sobotik M (1992) Wurzelatlas mitteleuropäischer Grünlandpflanzen. Verlag Gustav Fischer, Stuttgart, Jena, New York.

Lindborg R, Plue J, Andersson K, Cousins SAO (2015) Function of small habitat elements for enhancing plant diversity in different agricultural landscapes. Biological Conservation 169: 206–213. https://doi.org/10.1016/j.biocon.2013.11.015

Lukács BA, Török P, Kelemen A, Várbíró G, Radócz S, Miglécz T, Tóthmérész B, Valkó O (2015) Rainfall fluctuations and vegetation patterns in alkali grasslands – Self-organizing maps in vegetation analysis. Tuexenia 35: 381–397. https://doi.org/10.14471/2015.35.011

Maunder M (1992) Plant reintroduction: An overview. Biodiversity and Conservation 1: 51–61. https://doi.org/10.1007/BF00700250

Menges ES (2008) Restoration demography and genetics of plants: when is a translocation successful? Australian Journal of Botany 56:187–196. https://doi.org/10.1071/BT07173

Miglécz T, Tóthmérész B, Valkó O, Kelemen A, Török P (2013) Effect of litter on seedling establishment: an indoor experiment with short-lived Brassicaceae species. Plant Ecology 214: 189–193. https://doi.org/10.1007/s11258-012-0158-6

Plieninger T, Hartel T, Martín-López B, Beaufoy G, Bergmeier E, Kirby K, Montero MJ, Moreno G, Oteros-Rozas E, Van Uytvanck J (2015) Wood-pastures of Europe: Geographic coverage, social–ecological values, conservation management, and policy implications. Biological Conservation 190: 70–79. https://doi.org/10.1016/j.biocon.2015.05.014

Plieninger T, Dijks S, Oteros-Rozas E, Bieling C (2013) Assessing, mapping, and quantifying cultural ecosystem services at community level. Land Use Policy 33: 118–129. https://doi.org/10.1016/j.landusepol.2012.12.013

Ramos IL, Bernardo F, Ribeiro SC, Van Eetveld V (2016) Landscape identity: Implications for policy making. Land Use Policy 53: 36–43. https://doi.org/10.1016/j.landusepol.2015.01.030

Rout TM, Hauser CE, Possingham P (2009) Optimal adaptive management for translocation of a threatened species. Ecological Applications 19: 515–526. https://doi.org/10.1890/07-1989.1

Steffan-Dewenter I, Münzenberg U, Tscharntke T (2001) Pollination, seed set and seed predation on a landscape scale. Proceedings of the Royal Society B 268: 1685–1690. https://doi.org/10.1098/rspb.2001.1737

Sudnik-Wójcikowska B, Moysiyenko II, Zachwatowicz M (2011) The value and need for protection of kurgan flora in the anthropogenic landscape of steppe zone in Ukraine. Plant Biosystems 145: 638–653. https://doi.org/10.1080/11263504.2011.601335

Szilassi P, Bata T, Szabó S, Czúcz B, Molnár Z, Mezősi G (2017) The link between landscape pattern and vegetation naturalness on a regional scale. Ecological Indicator 81: 252–259. https://doi.org/10.1016/j.ecolind.2017.06.003

Tälle M, Deák B, Poschlod P, Valkó O, Westerberg L, Milberg P (2016) Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. Agriculture, Ecosystems & Environment 15: 200–212. https://doi.org/10.1016/j.agee.2016.02.008

Török P, Miglécz T, Valkó O, Kelemen A, Deák B, Lengyel S, Tóthmérész B (2012) Recovery of native grass biodiversity by sowing on former croplands: Is weed suppression a feasible goal for grassland restoration? Journal for Nature Conservation 20: 41–48. https://doi.org/10.1016/j.jnc.2011.07.006

Tóth E, Deák B, Valkó O, Kelemen A, Miglécz T, Tóthmérész B, Török P (2016) Livestock type is more crucial than grazing intensity: Traditional cattle and sheep grazing in short-grass steppes. Land Degrad Develop. https://doi.org/10.1002/ldr.2514

Valkó O, Deák B, Török P, Kelemen A, Miglécz T, Tóth K, Tóthmérész B (2016a) Abandonment of croplands: problem or chance for grassland restoration? Case studies from Hungary. Ecosystem Health and Sustainability 2(2): e01208. https://doi.org/10.1002/ehs2.1208

Valkó O, Deák B, Török P, Kirmer A, Tishew S, Kelemen A, Tóth K, Miglécz T, Radócz S, Sonkoly J, Tóth E, Kiss R, Kapocsi I, Tóthmérész B (2016b) High-diversity sowing in establishment gaps: a promising new tool for enhancing grassland biodiversity. Tuexenia 36: 359–378. https://doi.org/10.14471/2016.36.020

Wallin L, Svensson BM, Lönn M (2009) Artificial dispersal as a restoration tool in meadows: sowing or planting? Restoration Ecology 17(2): 270–279. https://doi.org/10.1111/j.1526-100X.2007.00350.x

Zhou Z, Bao W (2011) Levels of physiological dormancy and methods for improving seed germination of four rose species. Scientia Horticulturae 129: 818–824. https://doi.org/10.1016/j.scienta.2011.04.024

Supplementary material 1

Supplementary material 1

Authors: Orsolya Valkó, Katalin Tóth, András Kelemen, Tamás Miglécz, Szilvia Radócz, Judit Sonkoly, Béla Tóthmérész, Péter Török, Balázs Deák

Data type: (measurement/occurence/multimedia/etc.)

Link: https://doi.org/10.3897/natureconservation.24.20019.suppl1

Nature Conservation 24: 81–92 (2018)
doi: 10.3897/natureconservation.24.20650
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Comparative assessment of reproductive traits across different habitats in the endangered Webb's hyacinth (*Bellevalia webbiana* Parl.)

Giovanni Astuti[1], Gianni Bedini[1], Angelino Carta[1],
Francesco Roma-Marzio[1], Alberto Trinco[1], Lorenzo Peruzzi[1]

1 *Department of Biology, Unit of Botany, University of Pisa, Via Derna, 1 56126, Pisa, Italy*

Corresponding author: *Giovanni Astuti* (vanni.astuti@gmail.com)

Academic editor: *I. Steffan-Dewenter* | Received 28 August 2017 | Accepted 22 December 2017 | Published 5 January 2018

http://zoobank.org/2C2262DF-DCBF-493A-AE68-A9C90107BBAE

Citation: Astuti G, Bedini G, Carta A, Roma-Marzio F, Trinco A, Peruzzi L (2018) Comparative assessment of reproductive traits across different habitats in the endangered Webb's hyacinth (*Bellevalia webbiana* Parl.). Nature Conservation 24: 81–92. https://doi.org/10.3897/natureconservation.24.20650

Abstract

To pursue a proper conservation of narrow endemic species, the knowledge of basic reproductive strategies is crucial to plan adequate conservation activities. One of the most evolutionarily relevant and threatened Italian endemic is the Webb's hyacinth (*Bellevalia webbiana* Parl.). As the reproductive behaviour of this species and its connection with human impact are currently unknown, the aim of this study was to characterise the reproductive traits of the Webb's hyacinth in contrasting habitats. All the 5 known richest populations across the species range were investigated. Their reproductive strategies were inferred by measuring inflorescence height, fruit set, seed set and *P/O* ratio. Reproductive features varied greatly amongst stands and also in relation to the degree of human disturbance. However, in all cases, seed sets showed low values. *P/O* values point towards full xenogamy and it is concluded that effective cross-pollination may be the main mode of sexual reproduction in *Bellevalia webbiana*. The reasons for the low reproductive performances may reside in pollen limitation, Allee effect and/or intrinsic reduced fertility of the species. Given this scenario, conservation efforts for Webb's hyacinth should focus on maintaining large and relatively dense populations, to guarantee some chance of *in situ* survival.

Keywords

conservation, Endangered, fruit set, IUCN, *P/O*, seed set

Introduction

The Mediterranean basin is a well-known biodiversity hotspot (Myers et al. 2000) where, unfortunately, native plant diversity is highly threatened by environmental changes, notably human-induced changes in land use (Lee et al. 1995, McKinney 2002, Rossi et al. 2013). Within this context, Italy hosts about one third of the animal and half of the European plant taxa (Rossi et al. 2013). Amongst these taxa, the endemics are of particular importance (Siljak-Yakovlev and Peruzzi 2012), representing in Italy about 19% of the total vascular flora (Peruzzi et al. 2014). To pursue a proper conservation of these species, especially the narrow endemics, the knowledge of basic reproductive strategies is crucial in planning adequate conservation activities (Rossi et al. 2016). Indeed, as witnessed by IUCN categories (IUCN 2017), persistence of plant populations is intimately connected to generation time, so that life history studies usually feature an integrated approach uniting demography, reproductive biology and genetics in order to assess the persistence of plant populations in ecosystems (Ohara et al. 2006). Dealing with sexual species, reproductive success can tell a lot about plants' survival and responses to stress factors. However, in many narrow endemics, the paucity of available material (e.g. low number of individuals and flowers, inaccessible sites etc.) does not allow proper insight into reproductive performances, which also require extensive field works in order to take into account all the possible environmental and biological factors. Due to this impediment, the knowledge of the breeding system of threatened species is at least the first step for understanding to which threats they can most be subjected (e.g. habitat fragmentation, pollen limitation, Allee effect etc.).

Amongst the numerous Italian narrow endemic plants, arguably one of the most evolutionarily relevant and threatened, is the Webb's hyacinth (*Bellevalia webbiana* Parl., Asparagaceae, monocots; Chiarugi 1949, Borzatti von Loewenstern et al. 2013, Astuti et al. 2017). According to Gestri et al. (2010), the range of this bulbous perennial herb is restricted to an area of pre-Apennines (100–700 m a.s.l.) in Tuscany and Emilia-Romagna (Central Italy), with two disjunct population groups. Typical habitats for Webb's hyacinth are open fields and meadows, wood margins, olive groves and vineyards; during the last century, Webb's hyacinth disappeared from several historical localities due to human settlements (Gestri et al. 2010). For these reasons, this species is currently listed in The IUCN Red List of Threatened Species as Endangered (EN A2c) (Peruzzi and Carta 2011). Despite these contributions providing important information on the species' distribution, habitat and systematics, many ecological aspects, including the reproductive behaviour, are still unknown.

As a first attempt to fill this gap of knowledge, the aim of the present study is to characterise for the first time the reproductive traits of Webb's hyacinth. These traits were evaluated in contrasting habitats marked by different degrees of direct human impact and representative of the species' range. Particularly, the following questions were addressed: 1) which is the breeding system of the species? 2) Are reproductive performances different amongst populations?

Methods

Sampling sites

All the known richest populations of *Bellevalia webbiana* (five, each with *N* > 50 individuals) were included in the study (Table 1). These five populations also show different degrees and kinds of direct human impact: the habitat in Pratolino is an open olive grove near a much-frequented parking area, whose herbaceous-layer community is periodically cut. Uccellatoio represents a wood margin along a path, whose herbaceous layer is sporadically cut, but heavily dug by rooting of ungulates (especially wild boars). Tavarnuzze is an open herbaceous community surrounded by trees and shrubs and currently not managed by man. Faenza represents a wood margin along a path, within a private property (Apicoltura Lombardi), actively conserved by the owners. Finally, the population of Casola Valsenio occurs at the margins of a cultivated field. Despite the latter locality falling within the borders of the protected area "Parco Regionale della Vena del Gesso Romagnola", it certainly represents, together with Pratolino, one of the most humanly-impacted populations amongst those studied. The five study sites were visited three times during 2016: in February for a preliminary survey, in March for measuring and sampling inflorescences/flowers and in June for sampling fruits and seeds.

Plant traits

On 10–15 randomly selected individuals per population (those sampled in March differing from those sampled in June), data were collected on a number of reproductive traits. The following activities were carried out directly in the field in March 2016: *(a)* measurement of inflorescence height (cm) and *(b)* counting of flower number per inflorescence. Both these parameters are known to positively affect pollinator visits and pollen load (Pyke 1981, Andersson and Iwasa 1996, Donnelly et al. 1998), as well as herbivory impact (Sletvold and Grindeland 2008) and pre-dispersal seed predation

Table 1. Studied populations of *Bellevalia webbiana*.

Population	Municipality, Province, Region	Coordinates	Elevation (a.s.l.)
Pratolino	Vaglia, Florence, Tuscany	43.859745°N, 11.296976°E	464 m
Uccellatoio	Vaglia, Florence, Tuscany	43.859192°N, 11.293367°E	505 m
Tavarnuzze	Impruneta, Florence, Tuscany	43.720970°N, 11.226723°E	93 m
Faenza	Faenza, Ravenna, Emilia-Romagna	44.276015°N, 11.811606°E	147 m
Casola Valsenio	Casola Valsenio, Ravenna, Emilia-Romagna	44.242883°N, 11.671955°E	316 m

(Brody et al. 1997). In addition, two flowers showing not-yet dehiscing anthers were collected per raceme and their anthers were conserved under ethanol:glycerol 3:1 (v/v) solution in 1 ml Eppendorf vials. In June 2016, the fruit number per inflorescence *(c)* was counted in the field. Then, for each raceme, two fruits were randomly collected and conserved in separate small paper bags.

Later, in the laboratory, the two sampled flowers per individual were used to determine: *(d)* the ovule number (O) per ovary and *(e)* the estimated pollen-grain number per flower (P). The two sampled fruits per individual were used to count the seed number *(f)*. In order to estimate the pollen-grain number per flower, the protocol reported by Galloni et al. (2007) was followed, with slight modifications (Astuti et al. 2017): all the six anthers of each sampled flower, still under ethanol:glycerol solution in 1 ml Eppendorf vials, were sonicated for 1 min at 14 kHz by means of a Sonoplus Ultrasonic Homogeniser GM 2070. Just before the sonication, a few small grains of solid leucobasic fuchsin were added to the solution, in order to allow the staining of the pollen-grain walls, for easier counting. During the sonication, the vials were maintained in ice to avoid excessive warming and also retained there for 20–30 seconds after the sonication. Then, 1 µl of homogenised solution was collected with a micropipette and placed on a microscope slide for pollen-grain counting. Each microscope slide was fully counted three times and, based on these three replicates, a mean total number of pollen-grains per sample was obtained. The estimation of the total pollen-grains number per flower was obtained by multiplying this number by 1000.

Starting from the above cited parameters, the fruit set [*(c)*/mean *(b)* for each population) and the seed set [*(f)*/*(d)*] were calculated for each individual. These two parameters are useful measures of reproductive performances, especially if related to pollination activity (Aguilar et al. 2006). In those cases where the fruit number of a certain individual was higher than the mean flower number for its population, the fruit set was adjusted to 1 by default. Finally, for each individual, the P/O ratio (Cruden 1977) was calculated. The variation of this ratio is correlated to the breeding strategy of a given angiosperm species: the lower the value, the more the plant is autogamous and vice-versa (Cruden 1977). In this case, this indirect method was adopted for assessing the breeding system due to relevant problems in flowers handling and manipulation (e.g. bagging experiments) in the field, due to their small size and unsuitable architecture.

Statistics

All the obtained data were analysed using PAST 3.14 software (Hammer et al. 2001, Hammer 2016). As all the considered variables were not normally distributed (after Shapiro-Wilk test) and lacked homogeneity of variance (after the Levene test), then the non-parametric Kruskal-Wallis test, complemented by Mann-Whitney pairwise comparison with Bonferroni correction, was used for comparing inflorescence height, number of flowers and number of fruits amongst populations. For the fruit set and seed set, χ^2 test was carried out. Only p values ≤ 0.01 have been considered significant.

Table 2. Reproductive parameters measured in the five studied populations of *Bellevalia webbiana*. The measurements are reported as mean value ± standard deviation.

	Pratolino	Uccellatoio	Tavarnuzze	Faenza	Casola
Inflorescence height (cm)	17.24 ± 4.11	24.85 ± 8.02	29.65 ± 5.05	51.84 ± 21.73	27.96 ± 7.79
Number of flowers	44.13 ± 10.06	32.57 ± 9.09	40.60 ± 12.47	62.15 ± 17.77	33.60 ± 6.58
Number of fruits	0	16.00 ± 9.79	13.93 ± 7.59	49 ± 19.27	16.53 ±11.07
Number of ovules	6	6	6	5.93 ± 0.26	6
Number of estimated pollen grains	28,261.90 ± 12,720.79	33,928.57 ± 11,090.57	21,130.95 ± 7,445.44	28,965.52 ± 7,533.87	23,000.71 ± 11,279.55
Number of seeds	0	2.17 ± 1.32	2.20 ± 1.45	2.57 ± 1.41	2.33 ± 1.12
Fruit Set	0	0.50 ± 0.27	0.34 ± 0.19	0.74 ± 0.25	0.47 ± 0.26
Seed Set	0	0.36 ± 0.16	0.37 ± 0.17	0.43 ± 0.19	0.39 ± 0.13
P/O	4,710.42 ± 2,120.05	5,654.76 ± 1,848.35	3,521.82 ± 1,240.96	4,827.58 ± 1,255.59	3,833.32 ± 1,880

Results

All the measured values are summarised in Table 2. Generally, the Faenza population shows values of inflorescence height (Figure 1), flower number and fruit number (Figure 2) significantly higher (Mann-Whitney test with Bonferroni correction).

Some more complex relationships concerning statistical differences amongst populations were found for the estimated number of pollen-grains per flower (see also Figure 3) and, given that the ovule number remained almost constant, consequently also for *P/O* values (Table 2).

Due to heavy cutting of all the individuals of the Pratolino population before fructification time, the number of fruits and seeds produced there dropped to zero (Figures 3, 4). χ^2 revealed significant differences amongst the remaining four populations concerning the fruit set, whereas no significant differences concerning seed number and seed set were found (Figure 4). χ^2 test revealed significant differences in the fruit set for all the pairwise comparisons, except between Uccellatoio and Casola. The Faenza population showed the highest fruit set, whereas Tavarnuzze the lowest. In all the populations, the mean seed set value was below 0.5 (Table 2, Figure 4).

Discussion

It was possible to highlight that, in *B. webbiana,* the ovule number is almost constant, with 2 ovules in a row for each of the three ovary locules. This confirms previous reports for the genus (Speta 1998). The *P/O* values of the studied populations, despite some differences (Table 2), all fall in a range of values reported by Cruden (1977) as typical of fully xenogamous species. In *Bellevalia,* the vegetative propagation was never reported (Feinbrun 1940, Speta 1998). However, in a plant coming from Casola Valsenio and cultivated in laboratory, the production of a small bulbil detaching from the main bulb was observed. Accordingly, *B. webbiana* can occasionally reproduce by means of vegetative propagation.

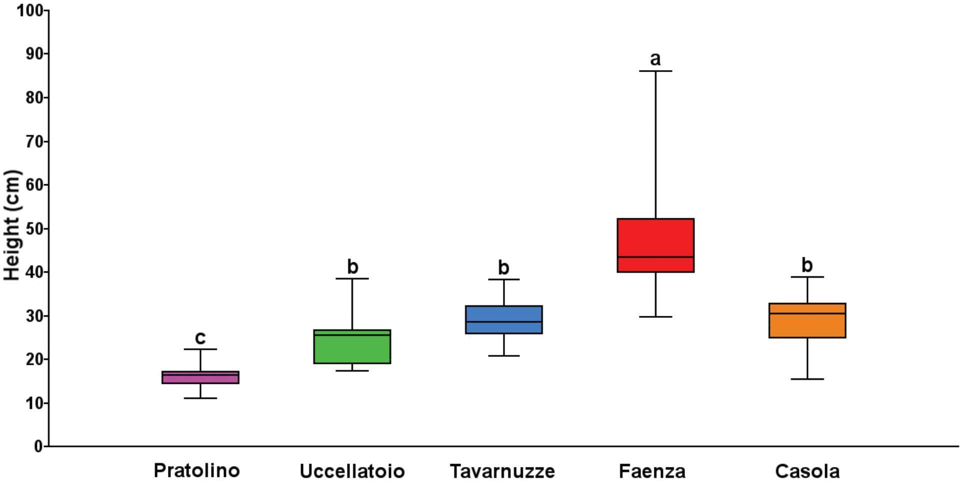

Figure 1. Boxplot of the inflorescence height (cm) in the studied *Bellevalia webbiana* populations. Different letters indicate statistically significant differences at 0.01 level.

The Faenza population, the only one actively conserved, shows several significant differences from other populations, concerning a higher reproductive effort (longer inflorescences with more flowers, more fruits and a higher fruit set; Figure 1, Table 2). This population is in close proximity to beehives and bees have been observed by the authors on Webb hyacinth's flowers during this research. However, despite the higher number of fruits produced and fruit set (Table 2, Figure 2), the seed set showed no significant differences compared to other populations (Tavarnuzze, Uccellatoio, Casola Valsenio; Figure 4). Although the effective contribution of bees in alleviating the possible pollen limitation was not quantified, the not-significantly higher reproductive success in this population may point towards other general problems, such as inbreeding depression or other intrinsic biological problems of the species.

On the other hand, there are the critical situations of Pratolino and Casola Valsenio. The reiterated periodical cutting in Pratolino population may easily explain the reduced size of inflorescences (Figure 1), due to lower nutrients stored in the bulb for the following year (Muller 1976, Werger and Huber 2006). Moreover, the cutting is, of course, the cause of the null reproductive outcome for this population. *Bellevalia webbiana* is perennial and long-living (a generation is estimated to be around 40 years by Gestri et al. 2010) and it is well known in literature that, in long-lived perennials, annual variation of reproductive success might be of minor importance (see, for instance, the study by Hoernemann et al. 2012 on *Muscari tenuiflorum* Tausch, a species from a genus phylogenetically close to *Bellevalia*). However, despite this, the reiterated reduction or absence of sexual reproduction might represent a relevant problem for the long-term survival of a species (Rathcke and Jules 1993). A general weakening of the individuals in the Casola Valsenio population may explain the slightly lower number of pollen-grains produced per flower (Figure 3). Indeed, still in 2010, this population was

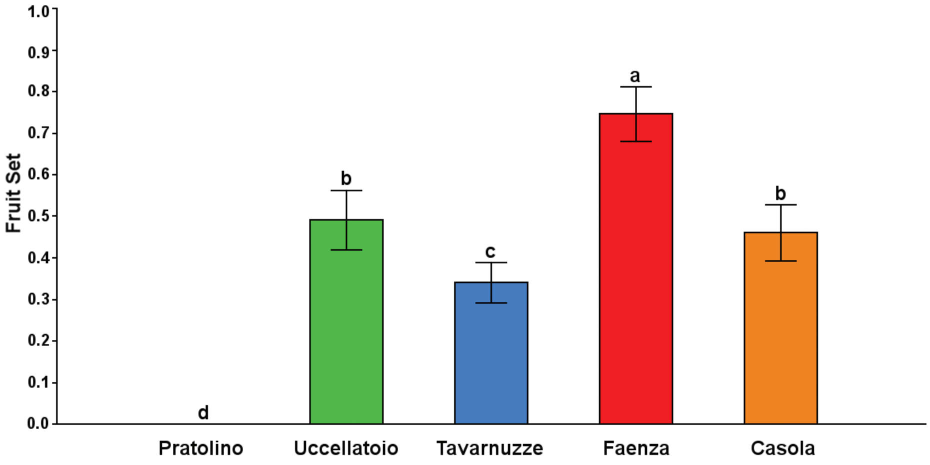

Figure 2. Box-chart of fruit set amongst the studied *Bellevalia webbiana* populations (confidence interval, 95%). Different letters indicate statistically significant differences at 0.01 level.

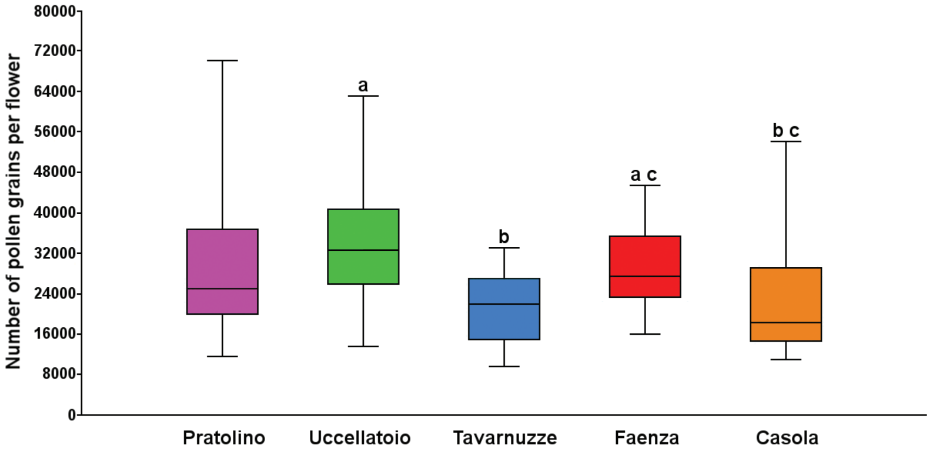

Figure 3. Boxplot of the estimated pollen grain number per flower in the studied *Bellevalia webbiana* populations. Different letters indicate statistically significant differences at 0.01 level.

made up of around 300 individuals (Gestri et al. 2010), but a very recent, improper, change in soil use decimated the population to a few tens of individuals at the margins and in-between the clumps of what is currently a ploughed field.

On the other hand, all the studied populations showed low seed set values in the 2016 flowering season (Figure 4). This result may point towards pollen limitation phenomena (Burd 1994). This appears likely, also considering the relatively early flowering period for this species, which often causes an unpredictable pollinator service

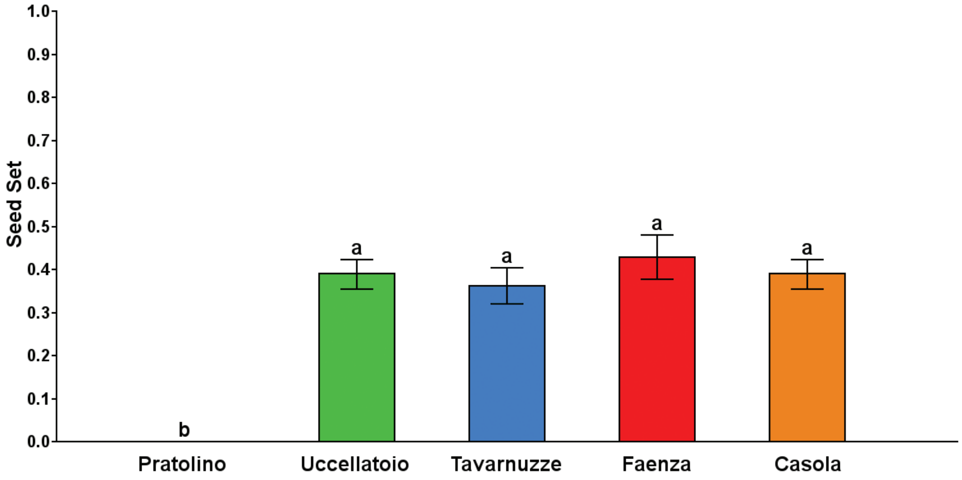

Figure 4. Box-chart of seed set in the studied *Bellevalia webbiana* populations (confidence interval, 95%). Different letters indicate statistically significant differences at 0.01 level.

(McCall and Primack 1992, Baker et al. 2000). Given that Webb's hyacinth seems xenogamous, it may also suffer some density-dependent fitness reduction, i.e. Allee effect (Courchamp 1999, Ashman et al. 2004), as observed in many other herbaceous entomophilous species (e.g. Kunin 1997, Schleuning et al. 2009, Hornemann et al. 2012). Another possible explanation for the low general reproductive performance is the occurrence of inbreeding depression due to isolation and fragmentation of the populations. Deleterious alleles, fixed by inbreeding depression, may easily cause abortion of fruits and/or seeds, especially during the earlier developmental stages (Wiens 1984, Rathcke and Jules 1993, Baker et al. 2000, Schleuning et al. 2007), or cause the production of low-quality pollen (Ashman et al. 2004). These phenomena could even more markedly affect the reproductive performance of smaller populations other than the five studied here, which are the richest currently known in terms of number of individuals. It is also noteworthy to state that the polyploid origin of this species is well documented (Chiarugi 1949, Borzatti von Loewenstern et al. 2013 and literature cited therein), so that intrinsic fertility problems for the Webb's hyacinth, due to its peculiar genomic constitution cannot be excluded. It is indeed well known that polyploidy can significantly reduce fertility in sexual reproduction (Levin 2002). Despite this, Capineri et al. (1979) documented for this species a regular meiosis with bivalents formation and this may lend support to different explanations for the low seed set (e.g. pollen limitation and/or Allee effect).

This study was conducted within a single year, providing thus a partial view of the reproductive behaviour of the species and its connection with human impact. However, these preliminary results already pointed towards urgent conservation issues, as habitat deterioration in several populations is progressing very rapidly. Given this scenario, conservation efforts for Webb's hyacinth should be devoted to maintain large and relatively dense populations, in order to guarantee some chance of *in situ* survival. The direct human impact on the sites (e.g. cutting etc.) should be allowed only after the seed dispersal, as this seems the prevalent reproductive method available to this species.

Further studies are necessary in order to check the reproductive performances in the medium-long period and to experimentally verify the hypotheses of possible (co-) occurrence of pollen limitation, Allee effect and/or intrinsic fertility problems of the species. In addition, it will also be useful to investigate the vegetative traits of Webb's hyacinth in relation to (especially human-induced) environmental changes. In the meantime, active *ex situ* conservation protocols have been established, by means of seeds stored in the Pisa Germplasm Bank (Italy) and in the Millennium Seed Bank, Kew Gardens (London, UK), complemented by propagation and cultivation in the Botanic Garden of the University of Pisa.

Acknowledgements

Mauro Lombardi from "Apicoltura Lombardi" is gratefully acknowledged, for logistic help and permission to work within his properties. We also thank the Director of the "Parco Regionale della Vena del Gesso Romagnola", for his support and permission to carry out this study. This work was funded by the "Progetto di Ricerca di Ateneo" (PRA) of the University of Pisa, under grant number PRA_2016_1.

References

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters 9: 968–980. https://doi.org/10.1111/j.1461-0248.2006.00927.x

Andersson M, Iwasa Y (1996) Sexual selection. Trends in Ecology and Evolution 11: 53–58. https://doi.org/10.1016/0169-5347(96)81042-1

Ashman T, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT, Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology 85(9): 2408–2421. https://doi.org/10.1890/03-8024

Astuti G, Brullo S, Domina G, El Mokni R, Giordani T, Peruzzi L (2017) Phylogenetic relationships among tetraploid species of *Bellevalia* (Asparagaceae) endemic to south central Mediterranean. Plant Biosystems 151(6): 1120–1128. https://doi.org/10.1080/11263504.2017.1320308

Astuti G, Roma-Marzio F, D'Antraccoli M, Bedini G, Carta A, Sebastiani F, Bruschi P, Peruzzi L (2017) Conservation biology of the last Italian population of *Cistus laurifolius* (Cistaceae): demographic structure, genetics and reproductive success. Nature Conservation 22: 169–190. https://doi.org/10.3897/natureconservation.22.19809

Baker AM, Barrett SCH, Thompson JD (2000) Variation of pollen limitation in the early flowering Mediterranean geophytes *Narcissus assoanus* (Amaryllidaceae). Oecologia 124: 529–535. https://doi.org/10.1007/s004420000417

Barrios-García MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biological Invasions 14: 2283–2300. https://doi.org/10.1007/s10530-012-0229-6

Borzatti von Loewenstern A, Giordani T, Astuti G, Andreucci A, Peruzzi L (2013) Phylogenetic relationship of Italian *Bellevalia* species (Asparagaceae), inferred from morphology, karyology and molecular systematics. Plant Biosystems 147: 776–787. https://doi.org/10.1080/11263504.2013.829884

Brody AK, Mitchell RJ (1997) Effects of experimental manipulation of inflorescence size on pollination and predispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. Oecologia 110: 86–94. https://doi.org/10.1007/s004420050136

Burd M (1994) Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. Botanical Review 60(1): 83–139. https://doi.org/10.1007/BF02856594

Capineri R, D'Amato G, Marchi P (1979) Numeri Cromosomici per la Flora Italiana: 534–583. Informatore Botanico Italiano 10(3)(1978): 421–465.

Chiarugi A (1949) Saggio di una revisione cito-sistematica della flora italiana I Il tetraploidismo della *Bellevalia webbiana* Parl e il suo diritto di cittadinanza nella flora italiana. Caryologia 1(3): 362–376. https://doi.org/10.1080/00087114.1949.10797519

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 10: 405–410. https://doi.org/10.1016/S0169-5347(99)01683-3

Cruden RW (1977) Pollen-ovule ratio: a conservative indicator of breeding systems in flowering plants. Evolution 31(1): 32–46. https://doi.org/10.1111/j.1558-5646.1977.tb00979.x

Donnelly SE, Lortie CJ, Aarsen LW (1998) Pollination in *Verbascum thapsus* (Scrophulariaceae): the advantage of being tall. American Journal of Botany 85: 1618–1625. https://doi.org/10.2307/2446490

Feinbrun N (1940) A monographic study on the genus *Bellevalia* Lapeyr (karyology, taxonomy, geography) (continued). Palestine Journal of Botany 1(4): 336–409.

Galloni M, Podda L, Vivarelli D, Cristofolini G (2007) Pollen presentation, pollen-ovule ratios, and other reproductive traits in Mediterranean Legumes (Fam Fabaceae - Subfam Faboideae). Plant Systematics and Evolution 266: 147–164. https://doi.org/10.1007/s00606-007-0526-1

Gestri G, Alessandrini A, Sirotti N, Carta A, Peruzzi L (2010) Contributo alla conoscenza della flora vascolare endemica di Toscana ed aree contermini 2 *Bellevalia webbiana* Parl (Asparagaceae). Informatore Botanico Italiano 42: 449–455.

Hammer Ø (2016) PAST version 3.14. http://folkuiono/ohammer/past/

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 1–9.

Hornemann G, Weiss G, Durka W (2012) Reproductive fitness, population size and genetic variation in *Muscari tenuiflorum* (Hyacinthaceae): the role of temporal variation. Flora 207: 736–743. https://doi.org/10.1016/j.flora.2012.07.005

IUCN (2017) Guidelines for using the IUCN red list categories and criteria. Version 13. Prepared by the Standards and petitions Subcommittee. http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf

Levin DA (2002) The role of chromosomal change in plant evolution. University Press, Oxford, 240 pp.

Lee H, Carr JL, Lankerani A (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation 4: 128–155. https://doi.org/10.1007/BF00137781

Kunin WE (1997) Population size and density effects in pollination: pollinators foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology 85: 225–234. https://doi.org/10.2307/2960653

McCall C, Primack RB (1992) Influence of flower characteristics, weather, time of day and season on insect visitation rates in three plant communities. American Journal of Botany 79: 434–442. https://doi.org/10.2307/2445156

McKinney ML (2002) Urbanization, Biodiversity, and Conservation. BioScience 52(10): 883–890. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

Muller RN (1978) The phenology, growth and ecosystem dynamics of *Erythronium americanum* in the northern hardwood forest. Ecological Monograph 48: 1–20. https://doi.org/10.2307/2937357

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

Ohara M, Tomimatsu H, Takeda T, Kawano S (2006) Importance of life history studies for conservation of fragmented populations: a case study of the understory herb, *Trillium camschatcense*. Plant Species Biology 21: 1–12. https://doi.org/10.1111/j.1442-1984.2006.00145.x

Peruzzi L, Carta A (2011) *Bellevalia webbiana*. The IUCN Red List of Threatened Species 2011: eT195349A8957996. http://dxdoiorg/102305/IUCNUK2011-2RLTST195349A8957996en

Peruzzi L, Conti F, Bartolucci F (2014) An inventory of vascular plants endemic to Italy. Phytotaxa 168(1): 1–75. https://doi.org/10.11646/phytotaxa.168.1.1

Pyke GH (1981) Effects of inflorescence height and number of flowers per inflorescence on fruit-set in waratahs (*Telopea speciosissima*). Australian Journal of Botany 29: 419–424. https://doi.org/10.1071/BT9810419

Rathcke BJ, Jules ES (1993) Habitat fragmentation and plant-pollinator interaction. Current Science 65(3): 273–277.

Rossi G, Montagnani C, Gargano D, Peruzzi L, Abeli T, Ravera S, Cogoni A, Fenu G, Magrini S, Gennai M, Foggi B, Wagensommer RP, Venturella G, Blasi C, Raimondo FM, Orsenigo S (2013) Lista Rossa della Flora Italiana 1 Policy Species e altre specie minacciate. Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma, 1–58.

Rossi G, Orsenigo S, Montagnani C, Fenu G, Gargano D, Peruzzi L, Wagensommer RP, Foggi B, Bacchetta G, Domina G, Conti F, Bartolucci F, Gennai M, Ravera S, Cogoni A, Magrini S, Gentili R, Castello M, Blasi C, Abeli T (2016) Is legal protection enough to ensure plant conservation? Italian red lists as a case study. Oryx 50(3): 431–436. https://doi.org/10.1017/S003060531500006X

Schleuning M, Niggemann M, Becker U, Matthies D (2007) Negative effect of degradation and fragmentation on the declining grassland plant *Trifolium montanum*. Basic Applied Ecology 10: 61–69. https://doi.org/10.1016/j.baae.2007.12.002

Siljak-Yakovlev S, Peruzzi L (2012) Cytogenetic characterization of the endemics: past and future. Plant Biosystems 146: 694–702.

Sletvold N, Grindeland JM (2008) Floral herbivory increases with inflorescence size and local plant density in *Digitalis purpurea*. Oecologia 34: 21–25. https://doi.org/10.1016/j.actao.2008.03.002

Speta F (1998) Hyacinthaceae. In: Kubitzki K (Ed.) The families and genera of vascular plants: flowering plants, Monocotyledons Lilianae (except Orchidaceae) 3. Springer-Verlag, Berlin, 261–285. https://doi.org/10.1007/978-3-662-03533-7_35

Werger MJA, Huber H (2006) Tuber size variation and organ preformation constrain growth responses of a spring geophyte. Oecologia 147: 396–405. https://doi.org/10.1007/s00442-005-0280-4

Wiens D (1984) Ovules survivorship, brood size, life history, breeding system, and reproductive success in plants. Oecologia 64: 47–53. https://doi.org/10.1007/BF00377542

Nature Conservation 24: 93–105 (2018)
doi: 10.3897/natureconservation.24.20538
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Effects of post-fire logging on California spotted owl occupancy

Chad T. Hanson[1], Monica L. Bond[2], Derek E. Lee[2]

[1] Earth Island Institute, 2150 Allston Way, Suite #460, Berkeley, CA 94704, USA **[2]** *Wild Nature Institute, 15 North Main Street #208, Concord, NH 03302, USA*

Corresponding author: *Chad T. Hanson* (cthanson1@gmail.com)

Academic editor: *R. Julliard* | Received 23 August 2017 | Accepted 18 December 2017 | Published 18 January 2018

http://zoobank.org/A8E84C32-7E27-4582-A5C6-86205CBF1566

Citation: Hanson CT, Bond ML, Lee DE (2018) Effects of post-fire logging on California spotted owl occupancy. Nature Conservation 24: 93–105. https://doi.org/10.3897/natureconservation.24.20538

Abstract

In fire-adapted forest ecosystems around the world, there has been growing concern about adverse impacts of post-fire logging on native biodiversity and ecological processes. This is also true in conifer forests of California, U.S.A. which are home to a rare and declining owl subspecies, the California spotted owl (*Strix occidentalis occidentalis*). While there has been recent concern about the California spotted owl occupancy in large fire areas where some territories have substantial high-severity fire effects, the influence of post-fire logging on the California spotted owl occupancy has been investigated very little, leading to some uncertainty about interpretation of conflicting results in different large fires. Research has found these owls preferentially select high-severity fire areas, characterised by high levels of snags and native shrubs, for foraging in forests that were not logged after fire, suggesting that removal of this foraging habitat might impact occupancy. The authors assessed the effect of post-fire logging and high-severity fire, on occupancy of this subspecies in eight large fire areas, within spotted owl sites with two different levels of high-severity fire effects. They found a significant adverse effect of such logging and no effect of high-severity fire alone. These results indicate it is post-fire logging, not large fires themselves, that poses a conservation threat to this imperilled species.

Keywords

wildland fire, spotted owl, forests, logging, post-fire logging, fire severity

Introduction

In fire-adapted forests around the world, a growing body of research indicates reasons for conservation concerns about the impacts of post-fire logging on native biodiversity and ecological processes (Lindenmayer and Noss 2006, Lindenmayer and Ough 2006, DellaSala et al. 2015, Heneberg 2015). The conifer forests of western North America are no exception (Hutto 2006, Swanson et al. 2011, DellaSala et al. 2015).

For a rare owl subspecies, the California spotted owl (*Strix occidentalis occidentalis*) which lives in the low/middle-montane conifer forests of the Sierra Nevada mountains of California, U.S.A. and the mountains of southern California, the effects of post-fire logging have been little studied. Some research suggests reduced site occupancy which has been observed in at least one large recent fire, the King fire of 2014 in the central Sierra Nevada, may occur due to predominantly high-severity fire effects (Jones et al. 2016). However, distinguishing the effects of fire alone from those of post-fire logging remains a challenge.

Populations of this subspecies are declining (Conner et al. 2013) and a petition for listing under the U.S. Endangered Species Act is pending (Bond and Hanson 2014). Thus, it is important to understand the extent to which forest management activities such as post-fire logging may be affecting spotted owl populations.

California spotted owls have been found to preferentially select unlogged high-severity fire areas characterised by high snag basal area and shrub cover for foraging (Bond et al. 2009) or to forage in this forest type in proportion to its availability (Bond et al. 2016, Eyes et al. 2017). This is likely due to the small mammal prey base found in this "complex early seral forest" habitat (DellaSala and Hanson 2015). One study, conducted in the San Bernardino mountains of southern California, found that removal of burned foraging habitat due to post-fire logging adversely impacted spotted owl site occupancy (Lee et al. 2013). However, this issue has not been addressed in the Sierra Nevada, where most California spotted owls live.

In this study, this issue was investigated by analysing the effect of post-fire logging on occupancy of California spotted owl sites, burned in large fires throughout the range of the subspecies, as well as the effect of high-severity fires.

Methods

First, to address how large fires affect California spotted owl site occupancy, fires with the following characteristics were analysed: (1) over 10,000 hectares in size, (2) occurring primarily on U.S. Forest Service lands post-2000, (3) included multiple spotted owl sites burned in the fire and (4) occupancy data were gathered by or for the U.S. Forest Service on national forest lands within the fire's perimeter. The sampling unit was the site (1500 m radius around the historical centre of the territory). Locations of historical site centres come from U.S. Forest Service survey data, as described below.

All sites analysed in this study were located in mature mixed-conifer forest that had recently burned. This forest type is comprised of yellow pine (*Pinus ponderosa* or *Pinus jeffreyi*) mixed with sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Psuedotsuga menziesii*) and California black oak (*Quercus kelloggi*).

High-severity fires were defined as forest with RdNBR (Relativised differenced Normalised Burn Ratio) values >572 (Jones et al. 2016), equating to a median level of basal area mortality of trees of ~80% (Miller et al. 2009, Miller and Quayle 2015). RdNBR values are based on satellite imagery and pertain to the difference between pre-fire and post-fire reflectance of green foliage (Miller and Thode 2007). The Rapid Assessment of Vegetation Condition (RAVG) satellite imagery database employed by the U.S. Forest Service was used to assess fire severity (https://www.fs.fed.us/postfirevegcondition/whatis.shtml). The RAVG database did not include the four oldest fires, the McNally fire, the Old fire, the Butler2-Slide fire and the Moonlight-Antelope fire, so the Monitoring Trends in Burn Severity (MTBS) satellite imagery database (www.mtbs.gov) was used for these fires, adjusting the 572 threshold value in the RAVG system by multiplying it by 0.875 (i.e. yielding an RdNBR value of 500) to obtain the equivalent percentage of high-severity fire in the MTBS system as was used in RAVG (Miller and Quayle 2015).

The U.S. Forest Service's Region 5 biologists conducted or oversaw surveys for California spotted owls at known sites using an established protocol (USFS 1995). Protocol for a given visit to a site involved trained observers playing calls to elicit responses from territorial spotted owls at night at multiple call points at fixed locations, with each call point surveyed for >10 minutes. At each site, to infer non-occupancy, the protocol required six visits with no detections during one breeding season (this was the case for all but one of the owl sites), or three visits with no detections in each of two consecutive breeding seasons (this was the case for site TUO027). Protocol further required that surveyors temporarily discontinue or reschedule surveys during inclement weather, such as high wind or rain. The authors excluded sites that otherwise met these study criteria but did not have a sufficient number of visits (possibly due to access issues) to meet protocol requirements.

Occupancy data from these surveys were obtained both before and after post-fire logging from the U.S. Forest Service for the following fires that met the above criteria: the McNally fire of 2002 (Sequoia National Forest); the Old fire of 2003 (San Bernardino National Forest); the Moonlight-Antelope fire of 2007 (Plumas National Forest); the Butler2-Slide fire of 2007 (San Bernardino National Forest); the Chips fire of 2012 (Plumas National Forest), not including the western half of the fire area which re-burned the Storrie fire of 2000 and that had extensive post-fire logging more than a decade ago, a fact which could confound these results; the Rim fire of 2013 (Stanislaus National Forest); the King fire of 2014 (Eldorado National Forest); and the Lake fire of 2015 (San Bernardino National Forest) (Figure 1).

Sites that were occupied in the most recent spotted owl survey year prior to post-fire logging were analysed. For example, the most recent surveys on the San Bernardino

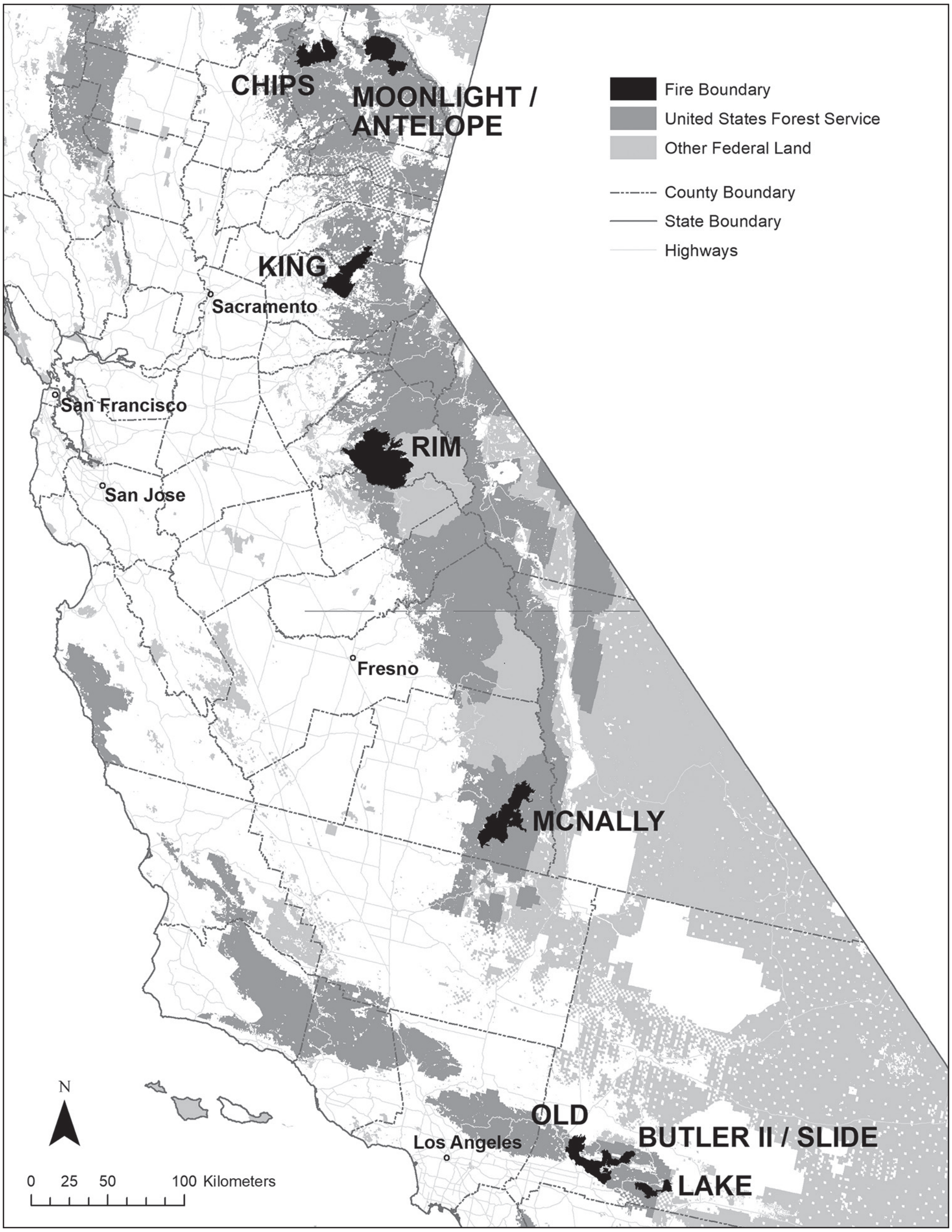

Figure 1. Large fires, in occupied California spotted owl habitat that were studied in this analysis.

National Forest (prior to the Lake fire of 2015) occurred in 2011, whereas in the Rim fire of 2013, surveys were sporadic prior to the fire, but were extensive beginning in the spring of 2014, prior to post-fire logging on national forest lands. The dates of fires, pre-logging and post-logging surveys and logging are shown in Table 1.

Table 1. Years in which the fires, pre-logging and post-logging surveys and logging occurred in each of the fires in this analysis.

Fire Name	Fire Year	Pre-/Post-Logging Surveys[1]	Logging
McNally	2002	2001/2004	Not applicable
Old	2003	2003/2005	Late 2003 through 2004
Moonlight-Antelope	2007	2006/2009	Late 2007 through 2008
Chips	2012	2012/2014	Late 2012 through early 2014
Rim	2013	2014/2016	Late 2014 through 2015
King	2014	2014/2015	Late 2014 through early 2015
Lake	2015	2011/2016	Not applicable
Butler2-Slide	2007	2007/2011	Late 2007 through 2010

[1] In the McNally and Lake fires, there was no post-fire logging in any of the spotted owl sites analysed in this study.

The authors considered a site to be occupied in a given year when at least one owl was detected (Lee et al. 2012, Lee and Bond 2015a, b, Jones et al. 2016). Detection indicated an owl utilised the site for any component of its life history, including foraging, roosting, nesting or territorial defence (Jones et al. 2016). Given the concern indicated in Jones et al. (2016) regarding lost occupancy in sites with substantial high-severity fire effects, the authors analysed naïve occupancy (detections versus no detections as recorded by surveyors, without extrapolating to adjust for probability of detection) of California spotted owl sites with 20–49% and 50–80% high-severity fire (as defined below). Occupancy of such sites was analysed within a 1500 m radius around site centres (nest or core roost locations at the centre of the site; Lee et al. 2012) at two different levels of post-fire logging, <5% and ≥5%, pertaining to the percentage of the total area within the 1500 m radius around the site's centre that was post-fire logged.

The radius distance of 1500 m around site centres was used as it has been found to be important to this subspecies for foraging (Bond et al. 2009). The authors chose 5% as the threshold for analysis of post-fire logging because this threshold, for logging in general, has previously been found to be associated with reduced California spotted owl occupancy (Seamans and Gutiérrez 2007). The effects of post-fire logging was not analysed for spotted owl sites with <20% high-severity fire because post-fire logging often does not occur in such sites. Conversely, the effects of post-fire logging were not analysed for sites with >80% high-severity fire because nearly all of these sites have ≥5% post-fire logging and there was not a sufficient number of such sites with <5% post-fire logging for the analysis.

To determine post-fire-logged areas, the U.S. Forest Service's FACTS database (http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833) was used which contains spatially explicit GIS data of post-fire logging activity in any given fire during any time period. The authors also used GIS data on fire severity (https://www.fs.fed.us/postfirevegcondition/whatis.shtml) and land ownership, where forested moderate- and high-severity fire areas on private lands are consistently post-fire logged, with rare exceptions. Post-fire logging in California's forests is a slightly modified form of clear-cutting, wherein nearly all fire-killed/scorched trees are removed (generally retaining ~10 snags/ha), except in low-severity fire areas which are typically not post-fire logged. Low-severity fire areas were excluded from post-fire logging polygons, with low-severity defined as RdNBR values <316 (Miller and Thode 2007). Google Earth was used, as well as physical inspections of the sites, to confirm post-fire logging. A remote private inholding in a large unroaded area in the Lake fire, which would otherwise have met the criteria described above and a private recreation inholding in the Rim fire were excluded, as no logging had occurred in either area. Similarly, some moderate/high-severity fire areas on larger private residential/recreational parcels had no post-fire logging in the Old fire and Butler2-Slide fire and such areas were not included in post-fire logging percentages.

In each of the two high-severity fire categories, the authors analysed whether post-fire logging affected spotted owl site occupancy using Chi-square tests for change in binomial proportions (Rosner 2000). A Chi-square test for change in binomial proportions was also used to analyse whether high-severity fire, without the influence of post-fire logging, affects site occupancy, restricting the analysis to sites with <5% post-fire logging and comparing occupancy of such sites with 20–49% high-severity fire to those with 50–80% high-severity fire.

Results

In sites with 20–49% high-severity fire (in terms of the percentage of the total area within a 1500 m radius around site centres with high-severity fire) and which were all occupied prior to post-fire logging, with <5% post-fire logging of the total area within a 1500 m radius of site centres, 12 of 15 spotted owl sites were occupied (80% occupancy). With 20–49% high-severity fire and ≥5% post-fire logging, 2 of 6 sites were occupied (33% occupancy) (Table 2). This difference was statistically significant ($c^2 = 4.23$, $P = 0.040$, DF = 1, $N = 21$ sites). To verify that this effect on site occupancy did not result from differences in high-severity fire, an *a posteriori* t-test for two independent means was conducted. In terms of percent high-severity fire, there were no differences between the <5% post-fire logging category (mean = 34.9%, SD = 7.7%, $N = 15$) and the ≥5% post-fire logging category (mean = 35.7%, SD = 11.0%, $N = 6$). This indicates that the difference in site occupancy was not due to different levels of high-severity fire ($t = -0.175$, $P = 0.863$). Amongst the sites with ≥5% post-fire logging, the mean amount of such logging of the area within a 1500 m radius of site centres was 17.5% (SD = 8.3%).

In sites with 50–80% high-severity fire and which were all occupied prior to post-fire logging, with <5% post-fire logging of the total area within a 1500 m radius of site centres, 10 of 13 spotted owl sites were occupied (77% occupancy). With 50–80% high-severity fire and ≥5% post-fire logging, only 4 of 20 sites were occupied (20% occupancy) (Table 3). This difference was statistically significant ($c^2 = 10.40$, $P = 0.001$, DF = 1, $N = 33$ sites). In terms of percent high-severity fire, there were no differences

Table 2. Occupancy of California spotted owl sites with 20-49% high-severity fire. Sites have varying levels of post-fire logging, within a 1500 m radius of territory centres, in large fires >10,000 ha in size since 2001. Within each fire, all sites were occupied in a single survey year prior to post-fire logging.

Fire	Site	% Post-fire Logging Category	% Post-fire Logging	% High-Severity Fire	Occupied?
Old	SB116	≥5%	24	49	N
Moonlight-Antelope	PL253	≥5%	26	40	N
Chips	Sta. 221/222	≥5%	8	26	Y
Chips	Sta. 223	<5%	0	27	Y
Chips	Sta. 207	≥5%	25	31	N
Rim	TUO010	<5%	3	40	Y
Rim	TUO011	<5%	4	39	Y
Rim	TUO024	<5%	2	36	Y
Rim	TUO026	<5%	4	25	Y
Rim	TUO039	<5%	4	33	Y
Rim	TUO040	<5%	2	44	Y
Rim	TUO078	<5%	2	30	Y
Rim	TUO085	<5%	3	45	Y
King	ELD009	<5%	4	23	N
King	PLA080	<5%	2	43	Y
King	S. Fork	<5%	4	24	N
King	PLA016	≥5%	10	22	Y
Lake	SB123	<5%	0	38	Y
Butler2-Slide	SB013	<5%	3	34	Y
Butler2-Slide	SB003	≥5%	12	46	N
Butler2-Slide	SB074	<5%	4	43	N

Table 3. Occupancy of California spotted owl sites with 50-80% high-severity fire. Sites have varying levels of post-fire logging, within a 1500 m radius of territory centres, in large fires >10,000 ha in size since 2001. Within each fire, all sites were occupied in a single survey year prior to post-fire logging.

Fire	Site	% Post-fire Logging Category	% Post-fire Logging	% High-Severity Fire	Occupied?
McNally	TU045	<5%	0	57	Y
McNally	TU047	<5%	0	59	Y
Old	SB084	≥5%	7	61	N
Old	SB089	≥5%	7	69	N
Old	SB065	≥5%	10	50	Y
Old	SB026	≥5%	27	79	N
Old	SB053	≥5%	12	66	N
Old	SB066	≥5%	18	53	N
Moonlight-Antelope	PL122	≥5%	15	53	N
Moonlight-Antelope	PL006	≥5%	17	65	N
Moonlight-Antelope	PL229	≥5%	11	66	N
Moonlight-Antelope	PL284	≥5%	23	71	N
Moonlight-Antelope	PL107	<5%	0	51	Y
Moonlight-Antelope	PL123	≥5%	11	59	N
Moonlight-Antelope	PL042	≥5%	8	71	N
Moonlight-Antelope	PL073	≥5%	10	57	N

Fire	Site	% Post-fire Logging Category	% Post-fire Logging	% High-Severity Fire	Occupied?
Moonlight-Antelope	PL125	≥5%	17	72	N
Chips	Mosquito	<5%	4	60	Y
Rim	TUO027	≥5%	39	59	N
Rim	TUO028	≥5%	24	77	Y
Rim	TUO177	≥5%	25	64	Y
King	ELD051	<5%	2	50	Y
King	PLA039	<5%	0	60	Y
King	ELD085	<5%	4	75	Y
King	ELD058	<5%	0	67	N
King	ELD057	<5%	1	63	N
King	Rd. 12N46	≥5%	30	52	N
Lake	SB021	<5%	0	77	Y
Lake	SB041	<5%	0	78	N
Lake	SB138	<5%	0	65	Y
Butler2-Slide	SB137	≥5%	9	55	Y
Butler2-Slide	SB060	<5%	2	57	Y
Butler2-Slide	SB014	≥5%	14	57	N

between the <5% post-fire logging category (mean = 63.0%, SD = 9.2%, $N = 13$) and the ≥5% post-fire logging category (mean = 62.8%, SD = 8.5%, $N = 20$), as determined *a posteriori* using a t-test for two independent means ($t = 0.064$, $P = 0.949$). This indicates that the difference in site occupancy did not result from different levels of high-severity fire. Amongst the sites with ≥5% post-fire logging, the mean amount of such logging of the area within a 1500 m radius of site centres was 16.7% (SD = 8.7%).

For sites with <5% post-fire logging within a 1500 m radius of site centres, there was no difference in occupancy between such sites with 20–49% high-severity fire and those with 50–80% high-severity fire ($c^2 = 0.034$, $P = 0.854$, DF = 1, $N = 28$ sites).

Discussion

These results indicate that substantial declines in California spotted owl occupancy following large fires are primarily driven by post-fire logging of complex early seral forest—a forest habitat type created by high-severity fire effects in mature conifer forests and which this subspecies has been found to select for foraging (Bond et al. 2009). Spotted owls likely forage in complex early seral forests because abundant dead trees for perch sites are available for this sit-and-wait predator (Carey and Peeler 1995) and the small mammal prey base can increase in such habitat, particularly deer mice (*Peromyscus maniculatus*; Zwolak 2009, Fontaine and Kennedy 2012, Borchert et al. 2014). Under this study design, all spotted owl sites were confirmed occupied prior to post-fire logging. While none of the categories analysed had 100% occupancy following post-fire logging, this is expected given that spotted owls often temporarily abandon sites occupied in the previous year, even where no logging or fire has occurred (USDA 1995). Thus, a portion of sites occupied in one year will not be occupied in the next. Conversely, a portion of sites not occupied in a given year may be re-colonised and occupied in the next year.

Concern has recently been expressed regarding the effect of large forest fires in the central Sierra Nevada on occupancy of the California spotted owl, particularly in sites with predominantly high-severity fire effects (Jones et al. 2016). Jones et al. (2016), who analysed the northern half of the 39,311 ha King fire of 2014, dismissed post-fire logging as a factor in the reduced spotted owl occupancy that they reported one year after the fire.

These results differ from those of Jones et al. (2016) in the King fire. There are some likely reasons for this difference. First, Jones et al. (2016) reported that a median of only 2% of the area within 1100 m circles around the site centres experienced post-fire logging based upon data obtained from privately owned forest management companies (Sierra Pacific Industries and Mason, Bruce & Girard Inc.). A mean of 6% post-fire logging within 1500 m circles was found (and a mean of 12% post-fire logging when sites with >80% high-severity fire are added), based on the methods described above, the FACTS database, Google Earth and physical inspection of the areas. This indicates a more pronounced role of post-fire logging when a larger portion of spotted owls' biological home range (Bond et al. 2009) is analysed. Second, Jones et al. (2016) reported that 8 sites, out of a total of 13 (Jones et al. 2016: figure 2) with >50% high-severity fire, experienced "site extinction" (i.e. were rendered unoccupied) due to the King fire. In fact these sites (PLA007, PLA065, PLA015, PLA109, PLA012, ELD060, PLA049 and PLA043) had not been occupied prior to the fire (based on spotted owl surveys conducted for the Forest Service, which were obtained from the agency). Many spotted owl sites have lost occupancy in recent years in this area likely due to extensive logging (Tempel et al. 2014). Thus, the conclusion by Jones et al. (2016), that the King fire caused the loss of occupancy in these sites, is not sound.

Jones et al. (2016) also reported that, for the foraging behaviour component of their study, spotted owls avoided high-severity fire areas, contrary to the findings of Bond et al. (2009). Jones et al. (2016) suggested that avoidance of high-severity fire areas may have explained reduced occupancy in sites with high levels of high-severity fire. However, Jones et al. (2016) did not account for distance from site centres for this central-place forager (Carey and Peeler 1995, Rosenberg and McKelvey 2009). They also included recent pre- and post-fire clearcut areas in their analysis of selection/avoidance of high-severity fire areas for foraging, rather than analysing foraging of intact, unlogged high-severity fire areas, as in Bond et al. (2009). Thus, the foraging behaviour results of Bond et al. (2009) and Jones et al. (2016) can be reconciled, given the owls' tendency to avoid clearcut areas (Call et al. 1992, Comfort et al. 2016), while selecting intact, unlogged high-severity fire areas dominated by an abundance of snags (standing dead trees) and shrubs (Bond et al. 2009).

Tempel et al. (2014) also reported an adverse effect of high-severity fires on California spotted owl site occupancy, mostly due to four sites that generally became unoccupied, or infrequently occupied, following the Star fire of 2001 on the Eldorado and Tahoe National Forests, amongst a sample size of 12 sites inside wildland fire areas.

However, these sites were heavily post-fire logged on both private timberlands and National Forest lands (Bond and Hanson 2014: Appendix C), a fact that was not reported by Tempel et al. (2014).

A common assumption has been that the occurrence of high-severity fires is increasing and is a major threat to the owl. This assumption is accompanied by recommendations for increased logging—especially "mechanical thinning"—on National Forest lands, intended to create low-density forests and reduce the potential for high-severity fires (Jones et al. 2016, Stephens et al. 2016). Post-fire logging and tree plantation establishment have also been promoted by the U.S. Forest Service in high-severity fire areas in an attempt to recover and restore mature, green forest cover (Peterson et al. 2015). However, these results and other research (Lee et al. 2013), indicate that post-fire logging of complex early seral forests is not consistent with California spotted owl conservation and mechanical thinning has been associated with dramatic and rapid population declines for this subspecies in the Sierra Nevada (Stephens et al. 2014). Further, multiple studies have indicated that there is no long-term increasing trend in high-severity fires in the Sierra Nevada (Hanson and Odion 2015, Keyser and Westerling 2017), or in the vast majority of the western U.S. (Keyser and Westerling 2017) since 1984.

The authors' finding, that spotted owl sites with predominantly high-severity fire effects had 77% occupancy when <5% of the area within a 1500 m radius of territory centres was subjected to post-fire logging, is notable in the sense that it compares favourably with current California spotted owl occupancy levels in unburned, mature forest (Lee et al. 2012). More post-fire research is needed pertaining to spotted owls, including investigations of time-since-fire. This is especially true for spotted owl sites with higher levels of fire severity, such as those with >80% high-severity fire within a 1500 m radius of site centres, which are uncommon compared to those with lower levels of high-severity fire. However, most of the relatively few owl sites with such high-severity fire levels in larger fires are subjected to substantial post-fire logging on both private and public lands, undermining potential for scientific understanding of the owl's relationship with such fire events. This will need to change in the future if one is to have sufficient data to analyse the effects of fire, versus the effects of post-fire logging, in sites with such levels of high-severity fire.

Conclusions

Adverse impacts to California spotted owl occupancy in large fires appear to be strongly influenced by post-fire logging, rather than fire alone. Increased logging of unburned forests has been proposed as a measure to curb fire behaviour (Jones et al. 2016), but such logging has been associated with a substantial and rapid loss of site occupancy (Stephens et al. 2014). Based on these results here and other research, it is suggested that such increased logging and the weakening of environmental protections that would be needed to facilitate it, are not a scientifically sound path forward towards recovery and conservation of declining California spotted owl populations.

Acknowledgements

We appreciate the thoughtful review of our manuscript, which improved it. We thank Tim Sinnott of GreenInfo Network for the GIS analysis conducted for this study. We are also grateful to the many U.S. Forest Service staff who conducted California spotted owl surveys and provided these data for analyses.

References

Baker WL, Hanson CT (2017) Improving the use of early timber inventories in reconstructing historical dry forests and fire in the western United States. Ecosphere 8: Article e01935. https://doi.org/10.1002/ecs2.1935

Bond ML, Hanson CT (2014) Petition to list the California spotted owl (*Strix occidentalis occidentalis*) as threatened or endangered under the federal Endangered Species Act. John Muir Project of Earth Island Institute, Big Bear City, CA, USA.

Bond ML, Lee DE, Siegel RB, Ward JP (2009) Habitat use and selection by California spotted owls in a postfire landscape. Journal of Wildlife Management 73: 1116–1124. https://doi.org/10.2193/2008-248

Borchert MI, Farr DP, Rimbenieks-Negrete MA, Pawlowski MM (2014) Responses of small mammals to wildfire in a mixed conifer forest in the San Bernardino Mountains, California. Bulletin of the Southern California Academy of Sciences 113: 81–95. https://doi.org/10.3160/0038-3872-113.2.81

Call DR, Gutiérrez RJ, Verner J (1992) Foraging habitat and home-range characteristics of California spotted owls in the Sierra Nevada. The Condor 94: 880–888. https://doi.org/10.2307/1369285

Carey AB, Peeler KC (1995) Spotted owls: resource and space use in mosaic landscapes. Journal of Raptor Research 29: 223–239.

Comfort EJ, Clark DA, Anthony RG, Bailey J, Betts MG (2016) Quantifying edges as gradients at multiple scales improves habitat selection models for northern spotted owl. Landscape Ecology 31: 1227–1240. https://doi.org/10.1007/s10980-015-0330-1

Conner MM, Keane JJ, Gallagher CV, Jehle G, Munton TE, Shaklee PA, Gerrard RA (2013) Realized population change for long-term monitoring: California spotted owl case study. Journal of Wildlife Management 77: 1449–1458. https://doi.org/10.1002/jwmg.591

DellaSala DA, Hanson CT (2015) Ecological and biodiversity benefits of mega-fires. In: DellaSala DA, Hanson CT (Eds) The ecological importance of mixed-severity fires: nature's phoenix. Elsevier Inc.,Waltham, MA, USA, 23–54. https://doi.org/10.1016/B978-0-12-802749-3.00002-5

DellaSala DA, Lindenmayer DB, Hanson CT, Furnish J (2015) In the aftermath of fire: Logging and related actions degrade mixed- and high-severity burn areas. In: DellaSala DA, Hanson CT (Eds) The ecological importance of mixed-severity fires: nature's phoenix. Elsevier Inc.,Waltham, MA, USA, 313–347. https://doi.org/10.1016/B978-0-12-802749-3.00011-6

Eyes SA, Roberts SL, Johnson MD (2017) California spotted owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape. The Condor 119: 375–388. https://doi.org/10.1650/CONDOR-16-184.1

Fontaine JB, Kennedy PL (2012) Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22: 1547–1561. https://doi.org/10.1890/12-0009.1

Hanson CT, Odion DC (2015) Sierra Nevada fire severity conclusions are robust to further analysis: a reply to Safford et al. International Journal of Wildland Fire 24: 294–295. https://doi.org/10.1071/WF14219

Heneberg P (2015) Case study: response of invertebrates to mixed- and high-severity fires in central Europe. In: DellaSala DA, Hanson CT (Eds) The ecological importance of mixed-severity fires: nature's phoenix. Elsevier Inc.,Waltham, MA, USA, 240–246.

Hutto RL (2006) Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conservation Biology 20: 984–993. https://doi.org/10.1111/j.1523-1739.2006.00494.x

Jones GM, Gutiérrez RJ, Tempel DJ, Whitmore SA, Berigan WJ, Peery MZ (2016) Megafires: an emerging threat to old-forest species. Frontiers in Ecology and Environment 14: 300–306. https://doi.org/10.1002/fee.1298

Keyser A, Westerling AL (2017) Climate drives inter-annual variability in probability of high-severity fire occurrence in the western United States. Environmental Research Letters 12: Article 065003. https://doi.org/10.1088/1748-9326/aa6b10

Lee DE, Bond ML (2015a) Occupancy of California spotted owl sites following a large fire in the Sierra Nevada. The Condor 117: 228–236. https://doi.org/10.1650/CONDOR-14-155.1

Lee DE, Bond ML (2015b) Previous year's reproductive state affects spotted owl site occupancy and reproduction responses to natural and anthropogenic disturbances. The Condor 117: 307–319. https://doi.org/10.1650/CONDOR-14-197.1

Lee DE, Bond ML, Siegel RB (2012) Dynamics of breeding-season site occupancy of the California spotted owl in burned forests. The Condor 114: 792–802. https://doi.org/10.1525/cond.2012.110147

Lee DE, Bond ML, Borchert MI, Tanner R (2013) Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto Mountains of southern California. Journal of Wildlife Management 77: 1321–1341. https://doi.org/10.1002/jwmg.581

Lindenmayer D, Noss R (2006) Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20: 949–958. https://doi.org/10.1111/j.1523-1739.2006.00497.x

Lindenmayer D, Ough K (2006) Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. Conservation Biology 20: 1005–1015. https://doi.org/10.1111/j.1523-1739.2006.00501.x

Miller JD, Thode AE (2007) Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109: 66–80. https://doi.org/10.1016/j.rse.2006.12.006

Miller JD, Knapp EE, Key CH, Skinner CN, Isbell CJ, Creasy RM, Sherlock JW (2009) Calibration and validation of the relative differenced normalized burn ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment 113: 645–656. https://doi.org/10.1016/j.rse.2008.11.009

Miller JD, Quayle B (2015) Calibration and validation of immediate post-fire satellite-derived data to three severity metrics. Fire Ecology 11: 12–30. https://doi.org/10.4996/fireecology.1102012

Peterson DW, Dodson EK, Harrod RJ (2015) Post-fire logging reduces surface woody fuels up to four decades following wildfire. Forest Ecology and Management 338: 84–91. https://doi.org/10.1016/j.foreco.2014.11.016

Rosenberg DK, McKelvey KS (1999) Estimate of habitat selection for central-place foraging animals. Journal of Wildlife Management 63: 1028–1038. https://doi.org/10.2307/3802818

Rosner BA (2000) Fundamentals of biostatistics. Duxbury (Pacific Grove, CA, USA).

Seamans ME, Gutiérrez RJ (2007) Habitat selection in a changing environment: the relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. The Condor 109: 566–576. https://doi.org/10.1650/8352.1

Stephens SL, Bigelow SW, Burnett RD, Collins BM, Gallagher CV, Keane J, Kelt DA, North MP, Roberts LJ, Stine PA, van Vuren DH (2014) California spotted owl, songbird, and small mammal responses to landscape fuel treatments. BioScience 64: 893–906. https://doi.org/10.1093/biosci/biu137

Stephens SL, Miller JD, Collins BM, North MP, Keane JJ, Roberts SL (2016) Wildfire impacts on California spotted owl nesting habitat in the Sierra Nevada. Ecosphere 7: Article e01478. https://doi.org/10.1002/ecs2.1478

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer D, Swanson FJ (2011) The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117–125. https://doi.org/10.1890/090157

Tempel DJ, Gutiérrez RJ, Whitmore SA, Reetz MJ, Stoelting RE, Berigan WJ, Seamans ME, Peery MZ (2014) Effects of forest management on California spotted owls: Implications for reducing wildfire risk in fire-prone forests. Ecological Applications 24: 2089–2106. https://doi.org/10.1890/13-2192.1

USDA Forest Service (USFS) (1995) Spotted and Great gray owl survey protocols. USDA Forest Service Pacific Southwest Region. Vallejo, CA, USA.

Zwolak R (2009) A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. Forest Ecology and Management 258: 539–545. https://doi.org/10.1016/j.foreco.2009.05.033