Israel Journal of Ecology & Evolution, 2018
http://dx.doi.org/10.1163/22244662-06303003

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Is the prickly pear a '*Tzabar*'? Diversity and conservation of Israel's migrant species

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Abstract Human-assisted biotic migration is a hallmark of the Anthropocene. Populations introduced outside their native ranges ('migrant species') have commonly been viewed as a threat to be addressed with lethal control programs. Israel has a long history of anthropogenic changes, and conservation has typically focused on ameliorating direct human impacts rather than eradicating migrant species. However, this may be changing with the growing influence of invasion biology worldwide. We conducted a review of the diversity, conservation status, and academic attitudes toward Israel's migrant species (IMS). We identified 199 plants and animals from 85 families that have immigrated into Israel from across the globe, and 122 species from 64 families considered native to Israel that have emigrated to every bioregion and to two oceans, although few species have become cosmopolitan. The conservation status of most immigrant (84.9%) and emigrant (55.7%) species has not been assessed, and even the native ranges of eleven immigrants (5.5%) remains unknown. Of those assessed, 27% of immigrants are threatened or decreasing in their native ranges, and 62% of emigrants are globally decreasing or locally threatened and extinct. After accounting for local extinctions, immigration has increased Israel's plant and vertebrate richness by 104 species. Israel's immigrants are increasingly being viewed from an invasion biology perspective, with 76% of studies published in the past decade, reaching over a quarter of local conservation publications. Incorporating principles of compassionate conservation could help foster a more socially acceptable and morally grounded approach to the immigrant wildlife of the Middle East.

Keywords Anthropocene; biodiversity; compassionate conservation; invasion biology; novel ecosystem

"Yet the banks of the Jordan, it's like nothing has changed	"אבל על חוף ירדן כמו מאומה לא קרה
The same silence, and the same scenery	אותה הדומיה וגם אותה התפאורה
The grove of Eucalyptus, the bridge, the old barge	חורשת האקליפטוס, הגשר, הסירה
And the scent of saltbush upon the water"	וריח המלוח על המים"
The Eucalyptus Grove by Naomi Shemer (translation)	חורשת האקליפטוס נעמי שמר

Introduction

In recognition of the magnitude of human-driven environmental changes, our current epoch has been named the Anthropocene (Waters et al., 2016). One of the hallmarks of this epoch has been the rapid redistribution of species across the globe, starting about 200 years ago and accelerating in the last century (Hulme 2009). Populations introduced outside their native ranges (here referred to as *migrant species*, Box 1) now form significant components of ecosystems, transforming historic assemblages into 'novel ecosystems' (Hobbs et al., 2006). Human-assisted biotic migration is not a new phenomenon, particularly in regions with long histories of human travel and trade, such as the Middle East. However, in the last two centuries the rate of migrations, and the distances traversed, have rapidly grown (Davis & Thompson 2000; Simberloff et al., 2013).

In the past three decades, the view that migrant species are threats to biodiversity have solidified, in part because they have come to represent anthropogenic change (Chew & Hamilton 2011; Davis et al., 2011) but also because some populations have had undesired effects (Davis 2009). Red foxes (*Vulpes vulpes*) and wild cats (*Felis catus*), introduced to Australia, are considered drivers of extinctions of endemic small mammals (Johnson & Isaac 2009). The decline of endemic bird species is similarly associated with mammalian predators, such as rats (*Rattus* spp.), introduced to New Zealand (Duncan & Blackburn 2004). Biotic migrations also raise concerns on the potential threats posed by the transmission of infectious diseases and their vectors to humans, to domestic plants and animals, and to wildlife (Carroll 2011).

The field of invasion biology has developed within conservation with the aim of halting biotic migrations, suppressing and eradicating populations outside their historic ranges, and maintaining ecosystems in a pre-Anthropocene state (Chew & Hamilton 2011). Invasion biology is exerting a powerful and growing influence on conservation practices worldwide. The International Union for the Conservation

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of Nature (IUCN) formed the Invasive Species Specialist Group in 1994 to "*prevent, control or eradicate*" migrant species (www.issg.org, accessed March 2017). The group compiled a list of *100 of the World's Worst Invasive Alien Species* to bring global attention to migrant species many consider to be particularly damaging to conservation aims and to human utilities (Lowe et al., 2000). In some regions, particularly islands, conservation is focused almost exclusively on controlling and eradicating migrant species (Doherty & Ritchie 2016). Australia declared a "*war on cats*" in 2016 with the aim of killing 2 million wild cats by 2020 (Hillier 2016). New Zealand aims to eradicate all migrant predators by 2050 (Owens 2017). The European Commission brought into law a regulation on migrant species, which obligates member states to control wildlife considered "*invasive*" (Hulme 2016).

Criticisms of invasion biology have been growing from academics in a range of disciplines including ecology, conservation biology, evolutionary biology, history, environmental humanities, and ethics, as well as from the public. Proponents of invasion biology have been criticized for claiming, without sufficient evidence, that migrant species are "*the second greatest threat to biodiversity*" (Chew 2015), and for employing militaristic jargon, such as describing populations that have thrived after being moved by humans as "*invasions*" (Larson 2005). The premise of invasion biology – that migrant species are driving an "*ecological crisis*" – is hotly debated (Davis et al., 2011; Davis & Chew 2017). The majority of migrant populations are not known to have caused the types of effects that would justify such claims (Davis 2011), and many have effects viewed as beneficial (Schlaepfer et al., 2011). In a world considered to be in the midst of a sixth mass extinction (Barnosky et al., 2011), it is notable that local species richness (α diversity) has remained remarkably constant for the past century across the globe, in part due to migrant species replacing local extinctions (Dornelas et al., 2014).

Heightened levels of biotic migration in the Anthropocene could be acting as an important adaptation mechanism to rapid change, and a countercurrent to extinction. The distribution of several species is now mostly or exclusively outside their native ranges (Lees & Bell 2008; Marchetti & Engstrom 2016; Lundgren et al., 2017). New regions are thus providing refuge for species threatened in their native ranges, and harming migrant populations can threaten the conservation of these species globally. The predomesticated ancestor of the dromedary camel (*Camelus dromedarius*) was native to North Africa and the Levant before going extinct in the wild 4–5,000 years ago. Today, a population of about half-a-million wild dromedary camels are thriving in the deserts of Australia, originating from domestic individuals that were abandoned or escaped (Root-Bernstein & Svenning 2016).

Even where populations of migrant species have unwanted impacts, control and eradication are often impractical. Most migrant populations cannot be eradicated, and therefore lethal control programs typically have no end point (Carroll 2011). Over a century of eradication efforts of migrant lantana (*Lantana camara*) in Australia, India, and South Africa, has had no measurable effect on its spread and abundance (Bhagwat et al., 2012). Killing wildlife does not necessarily result in population declines and may even drive increased densities. Lethal control of wild cats in Tasmania, Australia, resulted in increased densities, probably due to surviving cats colonizing vacant territories (Lazenby et al., 2015).

Suppression or eradication of migrant populations has also triggered ecological cascades that create further harms. The eradication of cats from offshore islands of Australia and New Zealand led to population increases of rabbits and rats, harming native vegetation and birds (Rayner et al., 2007; Bergstrom et al., 2009). Even where threatened native species have increased their population size following lethal control of migrant species, recovery has not been lasting. For example, intensive poison baiting of red foxes in southwestern Australia resulted in a 20-year recovery of woylies (*Bettongia penicillata*), but the population subsequently collapsed, probably due to increased cat predation (Marlow et al., 2015). Native species can also be harmed by efforts to control migrant species upon which they have developed ecological dependencies. An intensive control program of hybrid *Spartina* in San Francisco, USA, did not benefit the targeted native vegetation, and caused a significant decline in an endangered bird (California clapper rail, *Rallus longirostris obsoletus*) that uses the tall, dense grass for cover and nesting (Buckley & Han 2014).

Israel provides an important case study with which to rethink the role of biotic migrations in Anthropocene ecologies. As an ancient epicenter of anthropogenic activities, this region has long experienced species migrations as it is situated on the crossroads of three continents (Africa, Europe, and Asia). The Middle East was one of the first places in the world where domestication began, leading to the agricultural revolution around 10,000 years ago, which drove accelerated human settlements, travel, and trade (Asouti & Fuller 2012). It was during this period about 8,000 years ago, for example, that the black rat (*R. rattus*) was introduced to Israel from Asia (Ruffino & Vidal 2010). Israel can therefore be readily defined as an 'ancient novel ecosystem' and it is arguably not possible to recreate or even identify a 'native' ecological configuration.

Twenty-first century Israel has one of the highest human densities in the world, the highest birthrate of any developed nation, and a highly urbanized population (Shoshany & Goldshleger 2002; Orenstein & Hamburg 2010; Alkema et al., 2011; Schaffer & Levin 2014). Land cover across Israel has been transformed in the past century from primarily open spaces, to intensive agriculture and urban development (Schaffer & Levin 2014). These direct human impacts have been the focus of conservation concerns (McDonald et al., 2008; Orenstein & Hamburg 2010). Migrant species in Israel have typically not been subjected to significant control or eradication efforts, and some are now deeply integrated in local cultures. The prickly pear (*Opuntia ficus-indica*), an immigrant plant originating in Central America, has come to symbolize both Jewish Israelis and Palestinians as *native* to this land. The '*Tzabar*' (צבר), in Hebrew, is a culturally significant word that means both prickly pear and a Jew that was born – and is therefore rooted – in Israel. The '*Sabr*'

(صَبْر), in Arabic, means both prickly pear and patience, and to some Palestinians also identifies the locations of their lost ancestral homes in Palestine (Bardenstein 1998; Dor 2017).

Attitudes to migrant species in Israel may be changing, however, with the growing influence of invasion biology on conservation research and policy globally (Kolar & Lodge 2001; Galil 2007; Roll et al., 2007; Roll et al., 2008; Dovrat et al., 2012). It is therefore timely to consider the potential conservation implications of biotic migrations in Israel from a novel ecosystem perspective, which values both historic and emerging ecological configurations. Here we review the taxonomic diversity, historic geographic origins, and conservation status of Israel's migrant species (IMS) to assess how biotic migration is influencing local and global species richness and persistence. We also assess changes in academic attitudes toward immigrant species in Israel in the past thirty years. Finally, we discuss the policy and ethics implications of shifting the response to migrant species from an invasion biology to a compassionate conservation perspective.

Box 1 – Terms Used in this Study

Common categorizations of populations and species based on their biogeographic history have been criticized for being normative, culturally-laden, and militaristic (Larson 2005; Chew 2009; Davis 2009; Chew & Hamilton 2011; Hillier 2016). We therefore chose to avoid loaded terms such as 'invasive species'. Instead, we strove to use value-neutral terms that describe the process of human-assisted biotic migrations. We recognize that even seemingly innocuous terms (e.g. 'native', 'species') can be loaded with cultural values (Chew & Hamilton 2011).

Emigrant – Populations whose origin range includes Israel and have been introduced into new regions since the advent of the Anthropocene. Includes species that were domesticated in the native region and that have established wild populations elsewhere (e.g. wild cat, *F. catus*).

Immigrant – Populations introduced into Israel since the advent of the Anthropocene.

Migrant – Populations that have been introduced outside their native ranges since the advent of the Anthropocene (both immigrants and emigrants). Includes only species with self-sustaining populations.

Native – Includes species that have evolved in the region and/or species introduced to the region prior to the advent of the Anthropocene (e.g. black rat, *R. rattus* in Israel).

Methods

Diversity and Conservation of Israel's Migrant Species

We assessed the taxonomic composition, geographic ranges, and conservation statuses of IMS. We compiled a list of plant and animal species that have established in Israel through human-assisted migration (*immigrant species*, Box 1) and a list of species considered native to Israel that have established populations outside their historic native ranges (*emigrant species*, Box 1). We recorded the number of orders and families represented by IMS as a measure of taxonomic diversity.

The lists were composed from the Global Invasive Species Database (ISSG 2015), the Invasive Species Compendium (CABI 2016), the Global Biodiversity Information Facility (GBIF 2016), and the IUCN Red List (IUCN 2017). The immigrant fish list was based on Roll et al. (2007). The emigrant species list was supplemented with the Israel Wild Flower Database (WFI 2016), the Red Books of Endangered Plants and Vertebrates of Israel (Dolev & Perevolotsky 2004; Shmida & Pollak 2007), the PLANTS Database (USDA & NRCS 2016), NAS database (USGS 2016), and FishBase (Froese & Pauly 2016). Post-domestic ('feral') species were compiled and analyzed separately. To ensure the list was as full and accurate as possible, we compared the databases and consulted the literature where discrepancies arose. To ensure accurate species taxonomy, we checked all migrant species for synonymy with the R package *taxize* (version 0.7.9) and manually.

We recorded the countries where immigrants are considered native, and the destination countries of emigrants. Based on this country-based distribution, the origins and destinations were assigned to the world's twelve terrestrial bioregions, which are comprised of the eleven bioregions identified by Holt et al., (2012) and Antarctica and its islands, and to the Earth's five oceans. We compared the relative cosmopolitanism of emigrants by the number of bioregion and ocean destinations of each species and taxonomic groups. Vertebrates were assessed by class (amphibian, bird, fish, mammal, reptile), but due to limited data, we merged all invertebrates and all plants.

We mapped the origins of immigrants, and the destinations of emigrants, and compared their richness in each terrestrial bioregion. We calculated the extent of IMS globalization by summing the number of bioregions of origin and destination, and we compared globalization between species and taxonomic groups. We excluded marine IMS from the maps due to geographic uncertainties. For immigrant species whose native range was not included in the databases, we conducted a literature search to assign native bioregions where possible, with the remainder listed as 'orphans'.

We recorded the global conservation status and population trends of IMS using the IUCN Red List, and for emigrant species we also included local conservation statuses using the Endangered Plants and Vertebrates in Israel Red Lists. We calculated the proportion of IMS that are threatened, including those listed as Near Threatened, and the proportion with decreasing population trends. We also assessed the proportion of Israel's endangered and extinct plants that have emigrated, and the contribution of immigration to plant and vertebrate richness in Israel. Invertebrates were excluded because there is currently no comprehensive assessment of these taxa in Israel. Data collection ended in September 2016.

Academic Attitudes to Israel's Migrant Species

We assessed the relative prominence of invasion biology in Israel's scientific literature over time by measuring publication rates in local and discipline journals. We searched for relevant articles published between 1985 and 2017 using the keywords "Israel", "invasive", "exotic", "weed", "introduced" and "alien". We searched through 9 sources focused on this region and topic, including 3 Israeli journals: Israel Journal of Plant Science (previously Israel Journal of Botany), Israel Journal of Ecology and Evolution (previously Israel Journal of Zoology), and Israel Journal of Entomology; 2 regional sources: the journal Mediterranean Marine Science, and the book Biological Invasions in Europe and the Mediterranean Basin (Di Castri et al., 1990); and 4 international journals: Biological Invasions, Aquatic Invasions, Management of Biological Invasions, and Applied Vegetation Science.

We counted the number of articles published on invasion biology in Israel each year to assess change in research effort. We also counted the number of new first authors publishing each year to assess whether the number of academics working in this field has changed. New authors were included in the year they published their first paper as first-named authors on our list and we excluded all subsequent papers in which they were first-named authors (co-authored papers were not excluded). For each 5-year

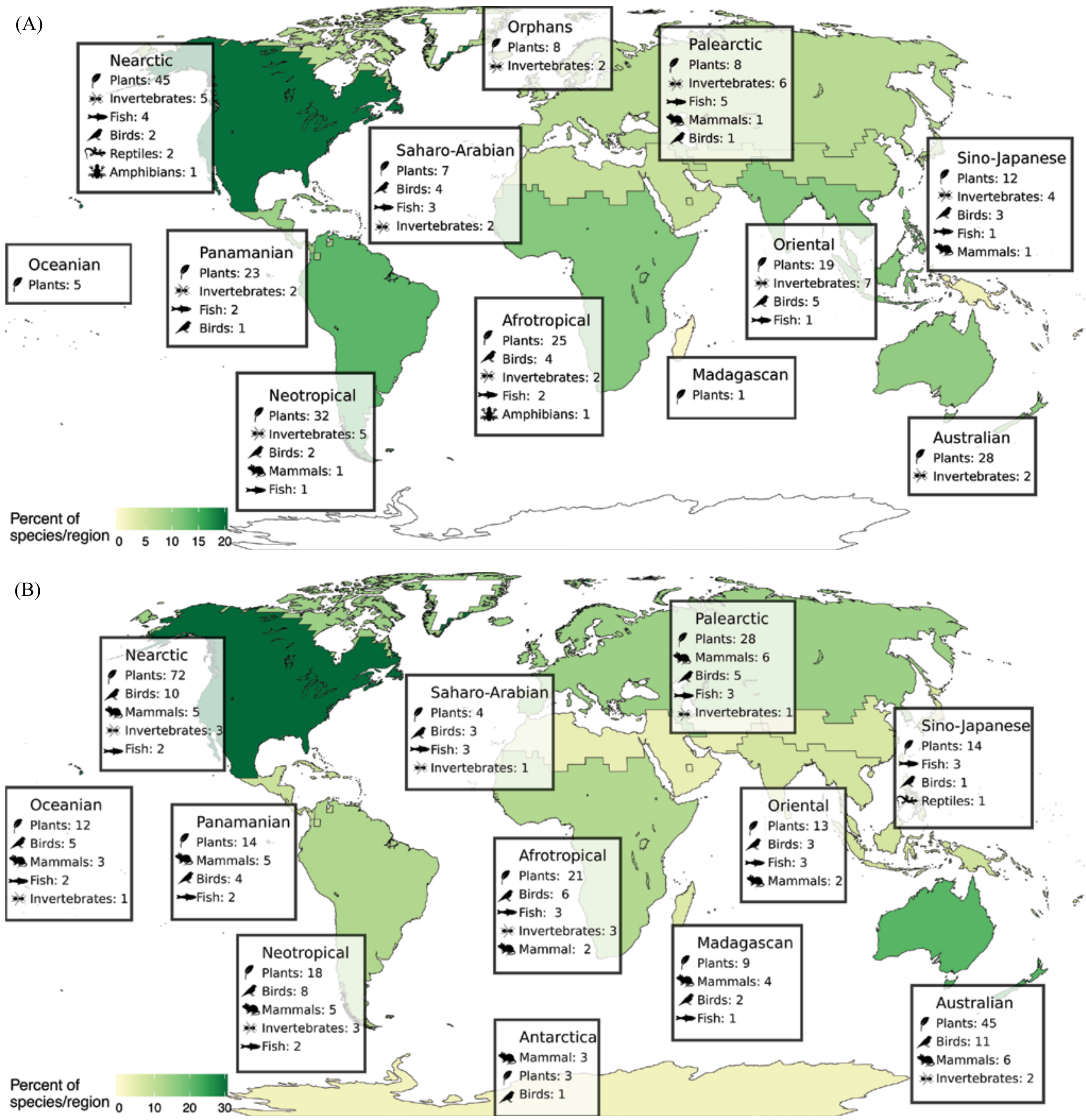


Figure 1. Israel's terrestrial migrant plant and animal species richness in each bioregion. (A) Historic native ranges of species that have immigrated into Israel. (B) Modern destinations of species native to Israel that have emigrated. Immigrant species whose native range is unknown are defined as 'orphans'. Delineation of bioregions was adapted from Holt et al., (2012).

period (apart from the incomplete 2015–2017 period), we calculated the average of both the number of invasion biology articles and the number of invasion biology authors published per year.

We measured the ratio of invasion biology to conservation publications in Israeli journals to assess the degree to which changing research effort in invasion biology reflects changing research effort in conservation. We conducted a search for articles using the keyword "conservation" in the selected Israeli journals and then compared the ratio of annual publication rates in conservation to that of invasion biology. Finally, we searched for articles using the keyword "novel ecosystem" in the selected Israeli journals to assess whether a diversity of views is being considered in the scientific literature on biotic globalization. The literature review ended in December 2017.

Results

We identified 199 immigrant species and 122 emigrant species (Table S1), representing a total of 120 families. Immigrant plants belong to 25 orders and 41 families, and immigrant animals belong to 28 orders and 44 families, with all vertebrate classes represented. Most immigrant species are plants (67.3%), followed by invertebrates (20.1%), and fish (5.5%). Emigrant plants belong to 27 orders and 42 families, and emigrant animals belong to 17 orders and 22 families, with reptiles and amphibians absent from vertebrate classes. Most emigrant species identified are plants (76.2%), followed by birds (12.3%), and mammals (5.7%).

IMS originate from, and have spread to, three of the world's five oceans and every major bioregion on Earth. Israel's immigrant species originate from three oceans, and from eleven of the world's twelve bioregions, most commonly from the Nearctic (30.7%) and Neotropical (20.6%) bioregions (Figure 1A). Eleven immigrant species (5.5%) are 'orphans', with unknown native ranges (Figure 2). The highest proportion of immigrant plants (33.6%) and animals (24.6%) originate from the Nearctic (Figure 1A). Israel's emigrant species have established in two oceans and in all of the world's bioregions, most commonly

Figure 2. 'Orphan species', whose native range is unknown, that have immigrated into Israel. The conservation status of these species is therefore also not known. Top panel left-to-right: chaff-flower (*Achyranthes aspera*), wild sandheath (*Centaurea eriophora*), marsh parsley (*Cyclospermum leptophyllum*), and coco grass (*Cyperus rotundus*). Middle panel left-to-right: goosegrass (*Eleusine indica*), asthma plant (*Euphorbia hirta*), tubeworm (*Ficopomatus enigmaticus*), and morning glory (*Ipomoea cairica*). Bottom panel left-to-right: obscure mealybug (*Pseudococcus viburni*), red palm mite (*Raoiella indica*), and rough cocklebur (*Xanthium strumarium*).

Images: *Achyranthes* by Jeevan Jose, *Centaurea* by Eusebiol, *Cyclospermum* by Forest & Kim Starr, *Cyperus* by Jeevan Jose, *Eleusine* by Tau'olunga, *Euphorbia* by Forest & Kim Starr, *Ficopomatus* by Duane Cox, *Ipomoea* by Earth100, *Pseudococcus* by Guy Buhry. Under license CC BY-SA 3.0/4.0, via Wikimedia.

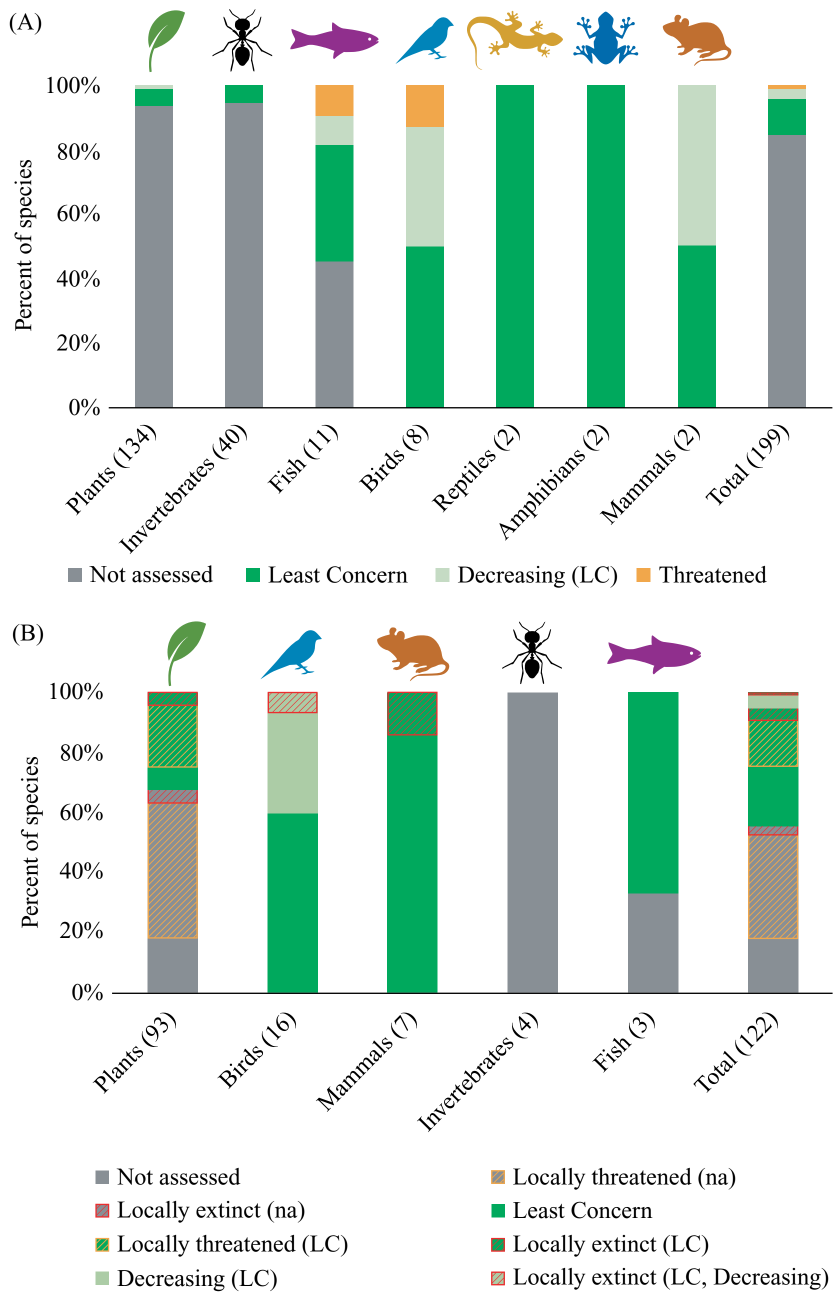


Figure 3. Conservation status of Israel's immigrant (A) and emigrant (B) species, in each taxonomic group. Threat statuses follow the IUCN Red List, and local (Israel) statuses are included for emigrant species (B). Colors denote global threat statuses according to the IUCN Red List, and for emigrant species also local threat statuses according to Endangered Plants and Vertebrates in Israel Red Lists.

in the Nearctic (75.4%), and Australian (52.5%) bioregions (Figure 1B). Most emigrant plants have established in the Nearctic (77.4%), and most animals established in the Nearctic (69%) and Australian (69%) bioregions (Figure 1B).

The most cosmopolitan emigrant taxa are fishes (3 species established in 8.7±1.2 bioregions), followed by mammals (7 spp., 5.9±0.6 bioregions), birds (15 spp., 3.9±0.2 bioregions), invertebrates (4 spp., 3.8±0.7 bioregions), and plants (93 spp., 2.7±0.02 bioregions). The most cosmopolitan emigrants (4 species, 3.3%) have established in 10 bioregions. These include two fishes (Israeli tilapia, *Oreochromis aureus*, and red belly tilapia, *Tilapia zillii*), one mammal (black rat, *Rattus rattus*), and one plant (castor oil plant, *Ricinus communis*). However, most emigrant species (81.2%) have established in 1–5 bioregions, with more than half (54.9%) established in just 1 or 2 bioregions.

The conservation status of most immigrants (84.9%) and emigrants (55.7%) is not known (Figure 3). Of the 30 immigrant species that have IUCN assessments, 2 (6.7%) are globally threatened (common carp, *Cyprinus carpio*, VU; and Alexandrine parakeet, *Psittacula eupatria*, NT) and an additional 6 (20%) are decreasing in their historic native ranges (Figure 4). Of emigrant species that have been assessed, 6 (11.1%) are decreasing in their historic native ranges. Additionally, 76 emigrants (62.3%) are listed as locally threatened in Israel, including 10 species that are extinct in Israel (Figure 5).

Figure 4. Immigrant species that are globally threatened or decreasing in their native ranges. Top panel from left to right: threatened species – common carp (*Cyprinus carpio*, Vulnerable), and Alexandrine parakeet (*Psittacula eupatria*, Near Threatened); and Least Concern (LC) but decreasing – golden carp (*Carassius carassius*), and Muscovy duck (*Cairina moschata*). Bottom panel from left to right, LC but decreasing: Indian silverbill (*Lonchura malabarica*), Nutria (*Myocastor coypus*), ruddy duck (*Oxyura jamaicensis*), and Sictus tree (*Tetraclinis articulata*). Photos: *Cyprinus* by Biopix, *Psittacula* by Sumatra Pramanick, *Carassius carassius* by Biopix, *Cairina* by Dario Sanches, *Lonchura* by Dibyendu Ash, *Myocastor* Petar Milošević, *Oxyura* Dick Daniels, *Tetraclinis* CS California via Wikimedia.

Figure 5. Emigrant species that are locally extinct in Israel. Top panel from left to right: Egyptian goose (*Alopochen aegyptiacus*), red deer (*Cervus elaphus*), soft bindweed (*Convolvulus pilosellifolius*), spreading bedstraw (*Galium humifusum*), and *Halopeplis amplexicaulis*. Bottom panel from left to right: dugong grass (*Halophila ovalis*), frogbit (*Hydrocharis morsus-ranae*), great yellowcress (*Rorippa amphibia*), slender clover (*Trifolium filiforme*), and water celery (*Vallisneria americana var. biwaensis*).
Images: *Alopochen* by Andreas Trepte CC BY-SA 2.5; *Cervus* by Charles Sharp CC BY-SA 4.0, *Convolvulus* by www.floraofqatar.com, *Galium* by Anatoly Lisitsyn, *Halopeplis* by Alon Solej CC BY-SA 3.0.

A significant proportion of Israel's threatened plant species have emigrant populations. Of 413 plants listed as locally threatened in Israel, 71 (17%) have established populations outside their historic range. After including historic extinctions, immigration has replaced and increased plant richness by 4.1% (from 2,424 to 2,522 plants) and vertebrate richness by 0.8% (from 771 to 777 vertebrates), increasing Israel's total plant and vertebrate richness by 104 species. Compared to 18 vertebrates that went extinct in Israel since the 19th century, 24 vertebrates have immigrated (Figure 6). This represents a total increase of 29% in amphibian richness (7 extant natives, 2 immigrants), 16% in freshwater fish richness (32 extant natives, 5 extinct natives, 10 immigrants), and 1% in bird

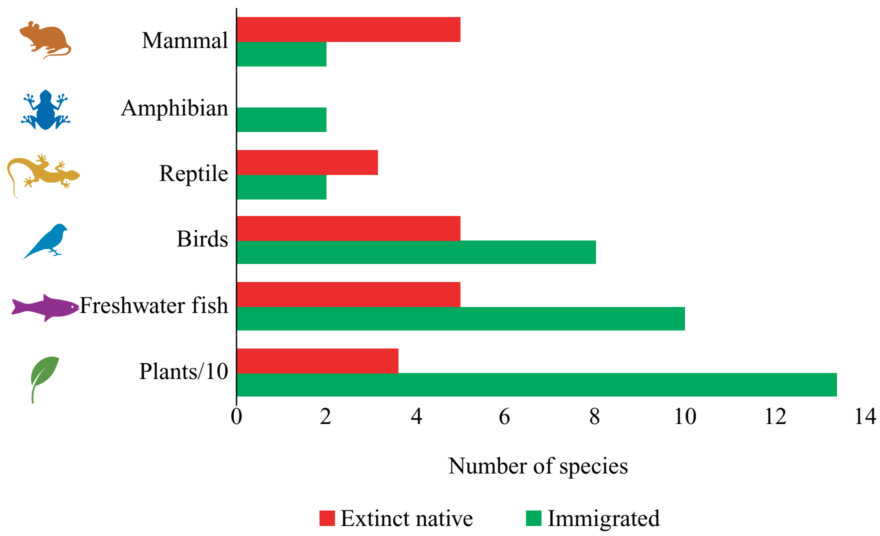
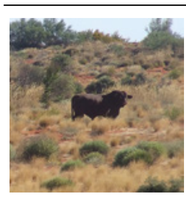
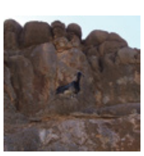
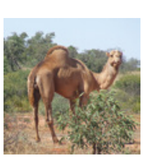
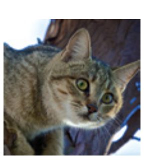
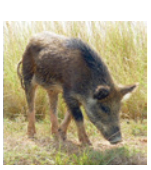


Figure 6. Number of plant and vertebrate species lost by extinction (red), and gained by immigration (green), in each taxonomic group in Israel since the late 19th century. Plant numbers were divided by 10 for scale.

Table 1 Post-domestic ('feral') animals that originated in Israel and surrounding region, and have established wild populations in new regions. The native ranges of most post-domestic species is not well defined, and their distinction as separate species to their pre-domestic ancestors is also often not clear. Conservation statuses refer to their pre-domestic ancestors in their native ranges, as Least Concern (LC), Vulnerable (VU), Extinct in the Wild (EW), and Extinct (EX). Photos by Arian Wallach (wild cattle, goat, camel), Angus Emmott (wild cat), and Agriculture Victoria (wild boar).

Post-domestics	Species name	Pre-domestic ancestor	Wild populations established (bioregions)	Global conservation status	Israel conservation status
	*Bos taurus*	*B. primigenius*	Australian, Nearctic, Neotropical, Oceanian, Oriental, Palearctic, Panamanian	EX	EW/EX
	*Capra aegagrus hircus*	*C. a.*	Australian, Madagascan, Nearctic, Neotropical, Oceanian, Palearctic, Panamanian, Saharo-Arabian, Sino-Japanese	VU	EX
	*Camelus dromedarius*	*C. thomasi*	Australian	EX	EW/EX
	*Felis catus*	*F. silvestris*	Afrotropical, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Palearctic, Panamanian, Saharo-Arabian, Sino-Japanese	LC	VU
	*Sus scrofa*	*S. s.*	Antarctica, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental, Palearctic, Panamanian	LC	LC

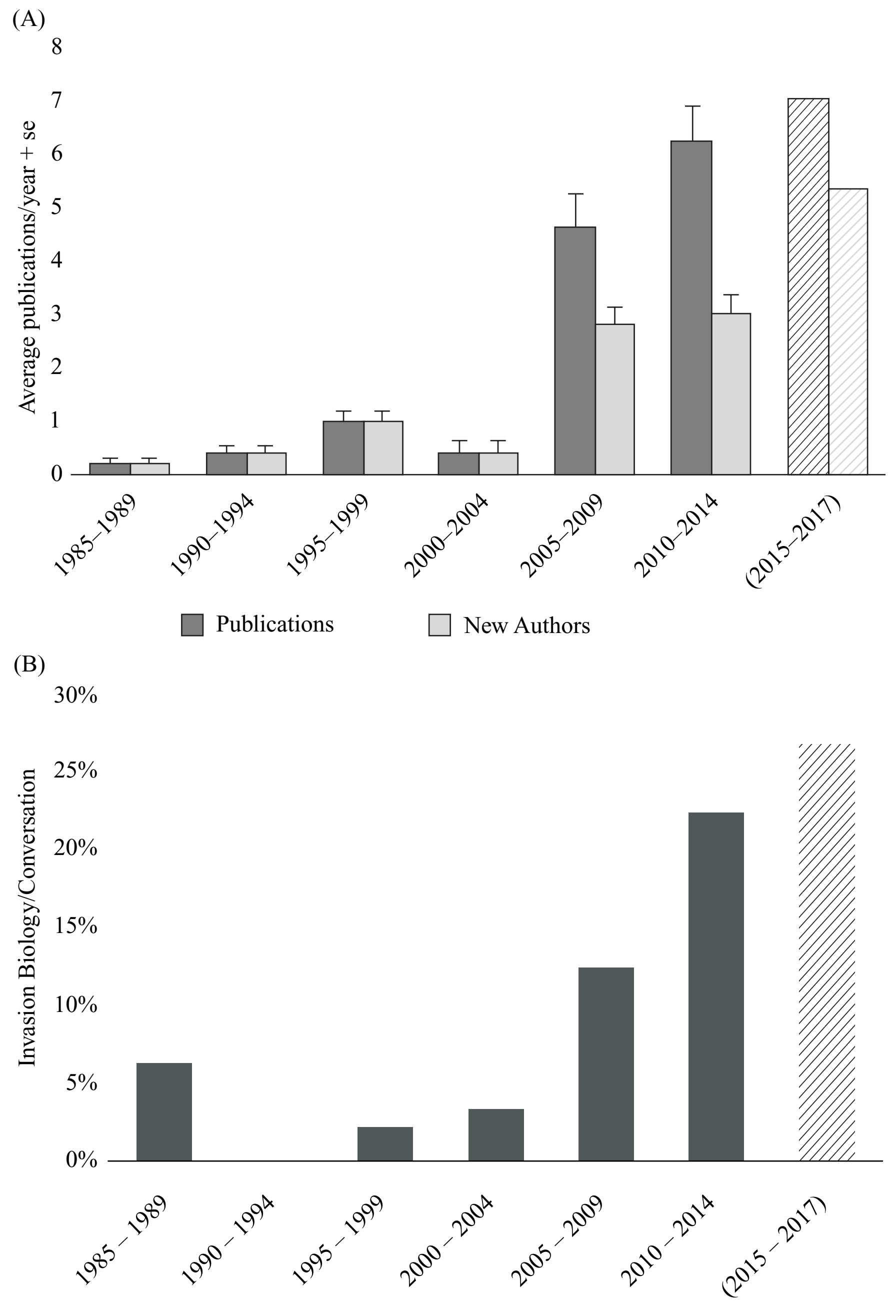


Figure 7. Publication rates that regard Israel's immigrant species from an invasion biology perspective. (A) The number of publications (dark grey), and the number new first authors (light grey), has grown in the past decade. (B) The ratio of invasion biology to conservation publications in Israeli journals has also grown in the past decade. Sources: Israel Journal of Plant Science, Israel Journal of Ecology and Evolution, Israel Journal of Entomology, Mediterranean Marine Science, Dafni and Heller 1990, Biological Invasions, Aquatic Invasions, Management of Biological Invasions, and Applied Vegetation Science. Dashed bars are for period <5 years.

richness (511 extant natives, 5 extinct natives, 8 immigrants). Despite supplementation by immigration, reptile richness has declined by ~1% (~100 extant natives, 3 extinct natives, 2 immigrants), and mammal richness has declined by 3% (103 extant natives, 5 extinct natives, 2 immigrants).

In addition to the 7 non-domestic emigrant mammals, an additional 5 post-domestic ('feral') mammal species whose ancestors are native to Israel have emigrated to 7.2±0.9 bioregions. There are no post-domestic immigrants in Israel. The conservation statuses of post-domestics (or their pre-domestic ancestors) include 1 that is Vulnerable, 2 that are Extinct, 2 that are Least Concern, and 3 that are locally threatened in Israel (Table 1).

Research that views Israel's immigrant wildlife from an invasion biology perspective has grown in the past decade. The literature review identified 85 studies since 1985 that refer to Israel's immigrants as 'invasive'. Of these, 76% were published in the past decade, reflecting an increase in both publications and new authors (Figure 7A). Within Israel's life sciences journals, the proportion of invasion biology publications (N=75) relative to conservation publications (N=541), has also increased markedly in the past decade to reach over a quarter of publications (Figure 7B). The literature review identified 7 studies that discuss novel ecosystems (5 of which on green roof urban ecology), with the first publication appearing in 2011.

Discussion

Our study joins the growing body of scholarship that migrant species are enriching the world in diverse and unexpected ways. Israel's migrant species (IMS) are taxonomically and geographically diverse, and many are globally or locally threatened in their assigned native ranges. Israel is a small country, yet its migrant species number at least 321 plants and animals, from 120 families. They have immigrated from, and emigrated to, every major bioregion in the world, and to three of the Earth's five oceans. The contribution of migrant populations to the persistence of species, and therefore to global species richness, requires significant attention. The conservation statuses of most of IMS, particularly plants and invertebrates, are not known. Exemplifying this conservation paradox are 'orphaned' species whose native ranges are unknown, which marks them as 'invasive' everywhere.

IMS challenge the notion that biotic migration drives global homogenization with few "winners" and many "losers" (McGill et al., 2015). Israel's 199 immigrant species are taxonomically diverse, comprised of members of 85 families, ranging from Australian trees to American and African amphibians, and from Indian parakeets to Atlantic Ocean fishes. Only 30 immigrants have conservation status assessments, and of those 27% are threatened or decreasing in their assigned native ranges. The 122 emigrants are comprised of members of 64 families, that have established around the world, although most have not become cosmopolitan. Most emigrants (62%) are locally or globally threatened and decreasing, including 10 species that are extinct in Israel (Figure 5), and 17% of Israel's threatened plants have emigrated.

The simultaneous decline of species in their native ranges and flourishing in their introduced habitats, suggests that migration is an important adaptation mechanism to anthropogenic changes (Lundgren et al., 2017). The Alexandrine parakeet is listed as Near Threatened due to population decline in their native range in Asia, caused by habitat loss, persecution, and trapping of wild birds for the pet trade (BirdLife-International 2016b). A small delimited population has successfully established in Israel (Roll et al., 2008). Nutria (*Myocastor coypus*) are listed by the IUCN as Least Concern but decreasing, they are locally endangered in parts of Argentina, and are absent from much of their native range across South America (Ojeda et al., 2016). Israel's immigrant nutria population has persisted for over five decades, and has even developed a uniquely long tail (U. Shanas unpublished). These new populations provide opportunities for ongoing evolution and speciation (Bull & Maron 2016).

Emigration has driven a global process of rewilding. Five mammal species whose pre-domestic ancestors are (or were) native to Israel have been introduced around the world as domestic animals, and eventually established wild populations: cattle (*Bos taurus*), goat, camel, cat, and boar. The pre-domestic ancestors of wild cattle (auroch, *B. primigenius*) and of wild camel (possibly *C. thomasi*) are extinct worldwide. These post-domestic wildlife are bringing back species richness and functions to many parts of the world (Root-Bernstein & Svenning 2016; Lundgren et al., 2017). The existence of these populations exposes the indeterminate and normative nature of concepts such as *native* and *wild* (Gibbs et al., 2015; Callaway 2016).

Species with large populations and ranges, including those undergoing positive population trends, can still be vulnerable to extinction. The IUCN lists the conservation status of red deer (*Cervus elaphus*) as Least Concern and their populations increasing (in their native ranges), and they have also been included in the *100 of the World's Worst Invasive Alien Species* list, attesting to their populations flourishing both inside and outside their assigned native range. However, red deer have not been immune to anthropogenic harms, and have been driven locally extinct from eleven countries and reintroduced into three (Lovari et al., 2016). In Israel, red deer went extinct in the 12th century at the end of a wave of megafauna extinctions, probably caused by human hunting and other impacts (Tsahar et al., 2009). Similarly, the house sparrow (*Passer domesticus*), one of Israel's secure emigrant species, and possibly one of the world's most well-known birds, is not immune to anthropogenic threats. They are listed by the IUCN as decreasing, red-listed as a species of high conservation concern in the UK, and Near Threatened in Germany, probably due to pesticide use and agricultural intensification (BirdLife-International 2016a). The decline of the house sparrow across its native range has prompted the formation of World Sparrow Day as a reminder of "*the beauty of the common biodiversity which we take so much for granted…* [that] *does not come with a lifetime guarantee*" (www.worldsparrowday.org).

Immigration has not only benefited individual species conservation on a global scale, but has also increased regional ecosystem richness and diversity. Over a fifth of Israel's freshwater fish and amphibian richness is now comprised of immigrants. Despite the extent of human population growth, urbanization, and habitat loss in Israel in the past century, plant and vertebrate richness has increased by about 104 species (after accounting for local extinctions). To the best of our knowledge, immigrants have not been 'accused' of driving native species extinct in Israel.

The contribution of immigration to biodiversity in Israel is consistent with patterns worldwide. Across the world's island ecosystems, migration has doubled plant richness, tripled freshwater fish richness, and stabilized bird richness (Sax & Gaines 2003). On continents, regional richness of plants and fishes has increased by 20% (Sax & Gaines 2003). Migrants have increased vascular plant richness from about 2,100 to 4,100 species in New Zealand, and from about 1,200 to 2,300 species in Hawaii (Sax et al., 2002). The world's terrestrial megafauna (body mass >100 kg), a globally imperiled group of species, are finding refuge outside their native ranges and increasing regional megafauna richness to well above Holocene levels (Lundgren et al., 2017). Overall, associations between the diversity of migrant and native plants tend to be positive (Sax & Gaines 2008; Thomas & Palmer 2015). The observation that ecosystems are continuing to absorb a growing number of species suggests that communities are not saturated (Sax et al., 2007) and that biodiversity is potentially boundless (Cornell 2013).

Invasion biology posits that migrant populations are likely harmful to native communities because they had not undergone long-term co-evolution. However, the growing number of observations of rapid adaptations in novel ecosystems challenges this assumption (Carroll 2011). The introduction of cane toads (*Bufo marinus*) to Australia has triggered rapid behavioral and morphological adaptation to their toxins, enabling native predators to recover from initial declines (Phillips & Shine 2004). Balloon vine (*Cardiospermum grandiflorum*) introduced to Australia was initially freed from consumers, but is now being predated on by the native Australian soapberry bug (*Leptocoris tagalicus*) who has rapidly evolved the necessary longer mouthparts to consume its seeds (Carroll et al., 2005). Rapid evolution has also occurred in Hawaii's native birds in response to the introduction of avian malaria and its mosquito vectors, enabling some species to recolonize low-elevation disease-prone regions (Woodworth et al., 2005).

Our study has shown that migration can contribute significantly to regional species richness, and to the survival of some species, to the extent that even a highly urbanized and populated country like Israel is increasing in plant and vertebrate richness. However, while regional species richness or diversity may increase, individuals, populations, and ecological processes can still be impacted negatively by human activities. There are many ways biodiversity trends can be measured and an increase in one can co-occur with a decline in another (McGill et al., 2015). It remains unknown, for example, what the population trends of Israel's migrant and native species have been since the advent of the Anthropocene. Thus, while the richness of some taxonomic groups may have grown, their overall population sizes and ranges may have contracted. The protection of habitat is one key component of conservation policy that can help ensure the foundation for evolutionary potential, for the wellbeing of many organisms, and for improving the ability of species to adapt to change. We have a moral obligation to consider the interests of other organisms alongside our own (Moore & Nelson 2011). Accepting novel ecosystems and migrant species, we argue, can enhance rather than diminish our commitment to respecting and protecting the natural world.

Compassionate Conservation of Israel's Immigrant Species

The growing influence of invasion biology on conservation in Israel is evident by the sharp increase in publication rate in the past decade that regard wildlife as invasive, taking up over a quarter of local conservation publications. This redirection of conservation attention from direct human impacts to immigrant species is at best a distraction. It is easier, after all, to cut down 'invasive' trees, than to protect Israel's remaining open spaces from human expansion and consumption. A plan to cut down *Eucalyptus* trees established in national parks for several decades has been strongly resisted (Arad 2017). Eucalypts, originating in Australia, were planted in Israel in its early nation-forming years, have since become an iconic part of the socio-ecological landscape. *The Eucalyptus Grove* by Naomi Shemer (quoted above) is one of Israel's most celebrated songs.

There are a wide range of perspectives on the phenomenon of species redistribution, how to respond to the presence of immigrant wildlife, and how to solve conflicts that arise in conservation, health, and agriculture. Invasion biology offers but one perspective that aims to return ecosystems to pre-anthropogenic conditions, by eradicating migrant species. This ideal is arguably elusive or even illusory in any part of the world, particularly in a region that has been an epicenter of human activity for millennia.

Israel has yet to embrace invasion biology. Its rise in academic circles has come some 20 years later than most (Kolar & Lodge 2001; Simberloff 2011), and largescale lethal programs have yet to be applied. This provides an opportunity for reflection before entrenching policies that are harmful, divisive and difficult to reverse. Invasion biology policies favor lethal control and are indifferent to animal welfare (Ramp & Bekoff 2015), which is unlikely to be widely accepted by Israeli society that is committed to animal protection (expressed in Hebrew as צער בעלי חיים, tza'ar ba'alei chaim) (Ruby 2012; Diemling 2015; Wolfson 2016). Several conservation programs based on killing wildlife, established in other parts of the world, contradict Israel's animal welfare policies. For example, alley cats have strong legal protections in Israel (Brickner-Braun et al., 2007). Policies that deliver benefits across all levels of biodiversity – from individuals to ecosystems – are more ethically defensible and more likely to be socially acceptable.

Compassionate conservation is a field dedicated to developing and promoting practices that are consistent with four guiding principles: *First, do no harm*, *Individuals matter*, *Valuing all wildlife*, and *Peaceful coexistence*. These principles provide an ethically robust approach to conservation challenges, including how to respond to immigrant populations. *First, do no harm*, the core precept of medical bioethics, was adopted as the first principle of compassionate conservation (Bekoff 2013). It serves as a caution that, "*given an existing problem, it may be better not to do something, or even to do nothing, than to risk causing more harm than good*". Ecosystems are extraordinarily complex. Simplistic and drastic actions, such as attempts to remove established immigrant populations, typically have unintended consequences.

The second principle, that the lives of *individuals matter*, is a recognition that sentience is a common traits in the animal kingdom, and that sentient beings should be treated with compassion (Vucetich & Nelson 2007). It is the individual, not the population, that experiences pain and pleasure. Harming the lives of individual animals cannot be ethically justified solely on the grounds of biogeographic origin, nor on notions of pristine nature. This principle requires that if immigrant populations have impacts deemed problematic, non-invasive approaches should be prioritized.

The third principle of compassionate conservation is *valuing all wildlife*, a commitment to respect the intrinsic value of all wildlife regardless of arbitrary classification (Dubois et al., 2017). The practice of eradicating migrant species to promote native species is incompatible with this principle. Unlike traditional conservation that values the native and the rare, compassionate conservation also values and aims to protect the immigrant and the common.

Finally, *peaceful coexistence* is the ultimate aim guiding compassionate conservation (Ramp & Bekoff 2015). It is a commitment that conservation is ultimately less about how we think the world should be and more about the manner in which we should engage with the world. This principle demands that the first action taken to solve problems involving immigrant species are modifications to our own practices (Dubois et al., 2017).

The principles of compassionate conservation are largely in line with many of Israel's established norms, and can therefore serve to strengthen positive practices and ethical commitments to wildlife. In contrast to invasion biology that was adopted relatively late, compassionate conservation established in Israel almost immediately. Several recent developments exemplify this: the first regional research group was founded in Israel (*Compassionate Conservation Middle East*) its members comprised of university and government scientists; the first regional compassionate conservation conference was hosted in Israel; and the first special issue on compassionate conservation is published in an Israeli journal. These suggest that a morally-grounded approach, which values and even embraces emerging ecological configurations, is well suited to 21st century Israel.

Acknowledgments

We thank Dror Ben-Ami for organising this special issue on compassionate conservation and for inviting this study. We appreciate the thoughtful comments of the anonymous reviewers on an earlier version of this manuscript that helped improve this work. We are also grateful to Uri Shanas and Matthew Chew for providing insights and discussions that were valuable in developing this work. This study grew out of the Compassionate Conservation Middle East Conference, hosted by the Dead Sea and Arava Science Centre, Hatzeva, Israel, in December 2016.

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