

How the Yellowhammer became a Kiwi: the history of an alien bird invasion revealed

Pavel Pipek¹, Petr Pyšek^{1,2,3}, Tim M. Blackburn^{4,5,6,7}

I Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Prague, Czech Republic 2 Institute of Botany, Department of Invasion Ecology, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic 3 Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, South Africa 4 Department of Genetics, Evolution & Environment, Centre for Biodiversity & Environment Research, Darwin Building, UCL, Gower Street, London WC1E 6BT, UK 5 Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK 6 Distinguished Scientist Fellowship Program, King Saud University, Riyadh 1145, Saudi Arabia 7 School of Earth & Environmental Sciences, University of Adelaide, SA 5005 Australia

Corresponding author: Pavel Pipek (ppipek@gmail.com)

Academic editor: Daniel Sol | Received 17 September 2014 | Accepted 13 November 2014 | Published 16 January 2015

Citation: Pipek P, Pyšek P, Blackburn TM (2015) How the Yellowhammer became a Kiwi: the history of an alien bird invasion revealed. NeoBiota 24: 1–31. doi: 10.3897/neobiota.24.8611

Abstract

New Zealand harbours a considerable number of alien plants and animals, and is often used as a model region for studies on factors determining the outcome of introductions. Alien birds have been a particular focus of research attention, especially to understand the effect of propagule pressure, as records exist for the numbers of birds introduced to New Zealand. However, studies have relied on compilations of bird numbers, rather than on primary data. Here, we present a case study of the alien yellowhammer (*Emberiza citrinella*) introduced from the UK to New Zealand, to demonstrate how recourse to the primary literature highlights significant data gaps and misinterpretations in these compilations. We show that the history of the introduction, establishment and spread of the yellowhammer in New Zealand can be reconstructed with surprising precision, including details of the ships importing yellowhammers, their survival rates on board, the numbers and locations of release, and the development of public perception of the species. We demonstrate that not all birds imported were released, as some died or were re-transported to Australia, and that some birds thought to be introductions were in fact translocations of individuals captured in one region of New Zealand for liberation in another. Our study confirms the potential of precise historical reconstructions that, if done for all species, would address criticisms of historical data in the evidence base for the effect of propagule pressure on establishment success for alien populations.

Copyright Pavel Pipek et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords

Bird invasion, establishment, introduction, invasion history, native range, New Zealand, propagule pressure, release, shipping

Introduction

Propagule pressure is widely accepted as one of the key factors determining the outcome of biological invasions (Lockwood et al. 2005, 2009; Duggan et al. 2006; Simberloff 2009; Blackburn et al. 2011b). If the numbers introduced are large enough, they have the potential to overcome the biological constraints of the invading species, and the intrinsic resistance of biological communities to the establishment of alien species (D'Antonio et al. 2001; Von Holle and Simberloff 2005). For these reasons, it has been suggested that propagule pressure should be used as a null model for studies of biological invasions that attempt to infer processes from patterns (Colautti et al. 2006). Unlike for plants, where metrics derived from the intensity of human activities (e.g. Daehler 2006; Křivánek et al. 2006; Chytrý et al. 2008) are usually used as proxies for propagule pressure (e.g. Wonham et al. 2013), analyses of bird invasions are often based on direct data on numbers derived from historical records of introductions (Blackburn et al. 2009). Nevertheless, the quality of data on bird propagule pressure is increasingly being questioned in the literature (Moulton et al. 2011, 2012a, b; Santos 2012), and this criticism has even been used to question the importance of propagule pressure as a key driver of establishment success.

The introduction of alien birds to New Zealand has been one of the key model systems for studying the effects of propagule pressure in historical data (e.g. Dawson 1984; Veltman et al. 1996; Duncan 1997; Green 1997; Sol and Lefebvre 2000; Cassey 2001; Duncan and Blackburn 2002; Brook 2004; Møller and Cassey 2004; Duncan et al. 2006; Blackburn et al. 2011a; Moulton et al. 2011). Bird introductions there started in the middle of the nineteenth century, under the auspices of a range of Acclimatisation Societies (Figure 1) founded with the express aim of naturalising alien species (McDowall 1994). New Zealand is an isolated archipelago, some 2,000 km from the nearest major landmass (Australia), and so introduced species had to be shipped there. Records from shipping and the Acclimatisation Societies mean that information on what was imported is relatively well delineated, compared to the situation in most continental areas. Nevertheless, the data on the importation and release of birds to New Zealand on which analyses of the effect of propagule pressure are based are not perfect, suffering from a variety of errors and problems of interpretation.

First, as pointed out by Moulton et al. (2012a), studies on the role of propagule pressure in bird introductions to New Zealand are mostly based, directly (e.g. Veltman et al. 1996; Blackburn et al. 2011a) or indirectly (e.g. Green 1997) through secondary sources (Long 1981; Lever 2005), on an influential book by the New Zealand





Figure 1. A map of New Zealand identifying the locations of the principal Regional Acclimatisation Societies.

naturalist George Malcolm Thomson. Thomson (1922) provides an extensive compilation of records of attempts to acclimatise species to New Zealand. Unfortunately, despite the volume of data it contains, the book suffers from significant information gaps. Thomson primarily based his research on the reports of the Acclimatisation Societies. These reports were sometimes poorly kept, and sometimes incorrectly interpreted by Thomson (1922). For example, a significant shipment of birds reached the Canterbury Acclimatisation Society in 1875, but in that year the Society did not pubΑ

ACCLIMATISATION SOCIETY.—It is a matter of congratulation to the mombers of this Society to know that the ship Tintern Abbey with a valuable consignment of birds, under the charge of Mr Henry Bills, has arrived, and that over 80 per cent of the birds shipped have come to hand. The following account has been furnished by Mr Bills; --Partridges shipped, 100; alive, 74. Blackbirds shipped, 117; all alivo. Thrushes shipped, 83; alive, 74. Xellow-hammers, 180; all alive. Redpoles, 120; all alive. Goldfinches, 110; all alive. Linnots shipped, 100; alive, 95. Starlings shipped, 100; alive, 11. It will thus be seen that a valuable lot of birds have arrived safely, thanks to the care taken by Mr Bills. The birds were forwarded to Christehurch by special train yesterday, leaving Lyttelton at 5 p.m., and were conveyed to the gardens. B

years 1875 and 1876. The Annual Report was printed in extenso in the leading news. papers of Canterbury, on the 23rd day of January, 1876, but it was never published in pamphlet form, nor was it circulated among the subscribers, owing to the fact that the Council deemed it impolitie to do so until the secounts were duly audited.

C

"It may be interesting to state that Mr Bills started from London with 1010 birds, and arrived at Lyttelton with 811, comprising 74 partridges. 117 blackbirds, 74 thrushes, 33 starlings, 180 yellowhammers, 120 redpoles, 110 goldfinches, 95 linnets, and 11 hedge sparrows; not a single goldfinch, yellowhammer, or redpole was lost on the voyage, and out of 100 linnets only 5 died.

"The Council are, however, sorry to report that the 500 leeches shipped were lost in the tropics.

Ε D F olack, Bramble Pruches Har Bills 1 Robson, margines + Chaffingles 95, Ban 33. JL Sep 14 Ball, Phease, Quail, Chaffinches 80. gellow to 6 Robson 40 magpies Billstopmma pies, g2pm min Evening Port Cypress Here Hod for mus

Figure 2. Examples of resources (extracts) used, five of which concern the shipment of birds on the Tintern Abbey. A Article about the arrival of the ship (Star 5 May 1875, Page 2) B the Twelfth and Thirteenth Annual Reports of the Canterbury Acclimatisation Society (Archives New Zealand, Christchurch Regional Office, CH1002/37/b) C The preliminary annual report published in a newspaper (Press 21 January 1876, Page 2) D letter of the Canterbury Acclimatisation Society confirming numbers E Minutes of the Canterbury Acclimatisation Society (Archives New Zealand, Christchurch Regional Office, CH1002/1/a) F Cashbook of the Wellington Acclimatisation Society (ref. number MSX-6860). Reprinted with the permission of the Christchurch Regional Office of Archives New Zealand (B, E), Christchurch City Libraries (D) and the National Library of New Zealand in Wellington (F).

lish its annual report in pamphlet form due to problems in accounts that had to be audited (Canterbury Acclimatisation Society 1877). The full text of the annual report was published only in a newspaper (Press 21 January 1876, Page 2), and information on the shipment is therefore not included in Thomson's book.

Second, the further in time from the date of publication of the original source of data on bird introduction, the higher the probability that those data will be interpreted erroneously. For example, Lever (2005) incorrectly interpreted the (already incomplete) data in Williams (1969) about introduction events in Canterbury, assuming that a request in 1873 by the Canterbury Acclimatisation Society for 108 yellowhammers (Star 23 March 1872, Page 2) was met. In reality, only 34 birds reached Canterbury in this shipment (Star 3 March 1873, Page 2).

Third, some of the birds released in New Zealand were actually born there, being captured in one part of the country and sold to another. These individuals were therefore not introduced, but rather translocated. For example, Thomson (1922) states that 32 yellowhammers were released on Stewart Island, and subsequent authors (e.g. Moulton et al. 2012a) count them as an introduction to New Zealand. These birds were, however, caught in Otago (Otago Daily Times 13 May 1879, Page 3). Translocations were even more prevalent in skylarks (*Alauda arvensis*). Williams (1969) says that 300 skylarks were distributed in South Canterbury in 1875, but these 300 birds were ordered from Nelson (Timaru Herald 29 October 1875, Page 4); furthermore only 165 of them survived (Timaru Herald 12 November 1875, Page 3)!

Fourth, some of the birds reported to have been introduced to New Zealand actually never made it into the wild: some died (e.g. Auckland Acclimatisation Society 1868; Daily Southern Cross 4 April 1871, Page 3), while others were re-transported to Australia (Press 27 March 1880, Page 3). Not surprisingly, given these complications, there is variation in the numbers of introduced individuals reported by individual authors (see Moulton et al. 2011); some works apparently underestimate the numbers (e.g. Thomson 1922; Lever 2005; Blackburn et al. 2011a), whilst others overestimate them for certain regions (Veltman et al. 1996; Duncan 1997). However, this of course raises the question of what was the actual number of birds introduced, and how much more accurate an estimate of this number can we get by mining historical sources?

Here, we explore data on historical introductions of the yellowhammer (*Emberiza citrinella*) to New Zealand, to show how much we can improve the knowledge of introductions if more sources, such as newspaper clippings and documents kept by Acclimatisation Societies (cashbooks, letters and minutes; Figure 2), are systematically explored. We aim to demonstrate how imprecise information can be propagated from one source to another, but that by going back to the primary sources of information (and avoiding "second-hand" resources), many uncertainties and inconsistencies that stem from using incomplete compilations can be eliminated (see also Moulton et al. 2011, 2012a; Haemig 2014). Finally, by correcting some erroneous data and pointing to misinterpretations in other treatments, we provide the most accurate information to date on yellowhammer introductions to New Zealand.

Methods

Newspapers

Newspapers from the 1840s onwards have been digitised by National library of New Zealand and made available online without any restriction through Papers Past (paperspast.natlib.govt.nz); this was launched in 2001, with 250,000 pages from historic New Zealand newspapers. New titles have been added regularly since then, and the whole site was re-launched in 2007 with a new interface that added full text search for a third of the collection. The whole collection was made searchable by mid-2009, allowing every short note referring to our focal species to be located. Newspapers have previously been used as data sources in ecological studies (Lamb 1964; Sowman 1981), but for obvious reasons, digitisation provides a major boost to their utility.

We searched Papers Past with search strings that included 'yellowhammer' in singular and plural, with/without a space between 'yellow' and 'hammer', and allowing for all sorts of possible typographical errors, which have been introduced to the text through the optical character recognition software used in digitisation (e.g. o or c instead of e, U instead of ll, b or li instead of h, v instead of y, rn instead of m, etc.). We also searched Papers Past for yel*mer*, as * represents any group of characters, again allowing for the aforementioned typographical errors.

After identification of ships bringing yellowhammers, and years of introduction, more directed keyword searches were used in order to understand the pathways by which the birds arrived (examples include: name of the ship; birds + liberated; Mr. Bills). Other details were searched directly, e.g. the address of certain purchasers of the birds, routes of ships. For additional information we also searched through archives of Australian (trove.nla.gov.au/newspaper) and British (newspaperarchive.com; www. bl.uk/reshelp/findhelprestype/news/newspdigproj/database) newspapers.

Resources kept by Acclimatisation Societies

In addition to the availability of newspaper archives, access to original data records made by Acclimatisation Societies is facilitated by the friendly attitude of New Zealand libraries towards researchers. We obtained the reports of three principal Societies – Auckland, Canterbury and Otago – from various libraries in New Zealand, which fully cover the period in which yellowhammers were introduced there (1863–1875). Beside reports, some Societies kept letter books, cashbooks and minutes, and we also obtained access to these records via the same libraries.

Other resources

There are also several original books and papers concerning bird introductions that date from the period when yellowhammers were being introduced to New Zealand (Taylor 1868; Hutton 1871; Wilson 1875) or from the early 1900s (Drummond 1906; Andersen 1916), including Thomson's well-known book and other compilations (Thomson 1922; Lamb 1964; Ashby 1967; Williams 1969; McDowall 1994; Veltman et al. 1996; Sullivan 1998). These sources served as a check on our searches of primary sources – if any information included in these secondary sources was new to us, we searched for its original source. We used information obtained from all of these resources to produce a comprehensive history of the introduction of the yellowhammer to New Zealand.

Results and discussion

Reasons for introduction

Contrary to common belief, fed also by some naturalists (Chrisholm 1907), yellowhammers and other small passerines were not introduced from Britain to New Zealand for sentimental reasons, but for a purely practical one: as a biological control agent to reduce the populations of insect pests (Wellington Independent 17 April 1852, Page 2; Lyttelton Times 19 February 1862, Page 3; Daily Southern Cross 4 April 1863, Page 3; Canterbury Acclimatisation Society 1867), most notably army worms (caterpillars of Mythimna separata) and black field crickets (Teleogryllus commodus) (Daily Southern Cross 19 March 1861, Page 3). Native bird species were obviously not able to do the job because their populations were retreating in step with their diminishing habitats (Wellington Independent 20 July 1865, Page 5). In 1868, Canterbury Acclimatisation Society even decided not to allow introductions of any animal species that were not useful for humans, in order not to waste the time of the Society's Curator (Canterbury Acclimatisation Society 1868). That said, the beauty of the yellowhammer's song was mentioned when the benefits of introductions were discussed in newspapers (Lyttelton Times 20 October 1864, Page 3). The pleasure derived from their songs, as a reminder of 'home', was a welcome bonus to the original pragmatic reason for introduction (New Zealand Herald 19 December 1872, Page 2).

It is rather surprising that the yellowhammer was introduced as a biological control agent for outbreaks of insect pests, as it is a mainly granivorous bird. Indeed, the list of species for introduction surprised even contemporary New Zealand naturalist Richard Taylor, who pointed out that the very same species (particularly sparrows) were targets of negative campaigns in their home country just a few years back (Taylor 1868). Yet, in New Zealand, the yellowhammer was initially regarded as a strictly insectivorous species (Otago Witness 15 October 1864, Page 4), desirable for introductions and protected by law (Nelson Examiner 12 January 1864, Page 6) and one of the most useful birds (Auckland Star 7 June 1870, Page 2). Yellowhammers were also regarded as beneficial (The Star, 10 January 1862, Page 1S) and almost purely insectivorous (Empire 12 July 1864, Page 2; Australian Town and Country Journal 25 June 1870, Page 19) in Australia. In 1863 the obvious granivory of yellowhammers, long known to British farmers (Quarterly Journal of Agriculture 7, 1837; Stephens 1851), was even questioned in England (The South Australian Advertiser 4 May 1863, Page 3, citing

Newry Examiner; Brighton Herald 26 November 1870). Despite early complaints by farmers (Lyttelton Times 22 January 1866, Page 4; Auckland Star 31 August 1875, Page 2), it took members of Acclimatisation Societies more than 15 years to realise their mistake; only as late as 1880 did the yellowhammer finally appear on the list of granivorous birds (North Otago Times, 13 March 1880, Page 2).

It would be tempting on the basis of this history to view the Acclimatisation Societies as peopled by amateurs, but this was far from the case. Their members included respected scientists, albeit with primary areas of expertise that did not encompass ornithology (e.g. botanists Thomas Kirk and Thomas Frederick Cheeseman – Auckland Acclimatisation Society 1873, 1876; doctor and historian Thomas Hocken – Otago Acclimatisation Society 1867; geologist Julius von Haast – Canterbury Acclimatisation Society 1866), as well as prominent members of government (e.g. the Governor of the New Zealand, George Grey – Otago Acclimatisation Society 1865; the Prime Minister of New Zealand, Frederick Weld – Canterbury Acclimatisation Society 1866), and thus may be viewed as relatively authoritative groups. Rather, this history illustrates the huge gap that existed between scientific and agricultural experience at the time, in England and New Zealand alike.

Capture in the native range

All yellowhammers imported to New Zealand were obtained in the United Kingdom, although we cannot rule out completely the possibility that some of them were caught in continental Europe and subsequently transported to UK markets, as was documented for goldfinches from Portugal (The Mercury 3 June 1871, Page 3). The origins of at least some of the yellowhammers are known with surprising precision. According to reports of the Otago Acclimatisation Society, only 39 yellowhammers came to Port Chalmers (Otago) and were released into nature (Fourth Annual report of the Otago Acclimatisation Society extracted from Otago Acclimatisation Society's Minutes; Otago Acclimatisation Society 1871). All these birds were personally collected in Brighton by Richard Bills (initially referred to as Edward Bills, although subsequent articles confirmed that Richard and Edward were one and the same), former respected bird fancier (Press 25 February 1871, Page 3), or several potentially by his wife (Otago Witness 8 February 1868, Page 5), and probably caught not far away from the city (Star 30 January 1871, Page 2); eight in 1868 (Daily Southern Cross 30 December 1867, Page 2; North Otago Times 4 February 1868, Page 2) and 31 from various districts around Brighton in 1871 (Press 25 February 1871, Page 3; Otago Witness 4 March 1871, Page 6). The first large transportation of yellowhammers to Canterbury (on the Charlotte Gladstone in 1873) was also arranged by Richard Bills (his services being more and more in demand, Otago Daily Times 4 May 1871, Page 3), and the birds were also collected in Brighton (Star 30 November 1872, Page 2). Later, an even larger transportation to Canterbury (on the Tintern Abbey in 1875) was organised by Richard's son Henry Bills, after his father retired to a sheep farm in Australia (Otago Witness 12 February 1876, Page 18). Henry



Figure 3. The total numbers of yellowhammers imported into individual regions of New Zealand. The piecharts show the proportions of birds with different fates (see inset legend).

lived in London when collecting birds (Press 20 January 1875, Page 2), and so the origin of these birds could therefore have been quite different.

Transport

In total, 25 ships can be identified heading to New Zealand with yellowhammers on board, all but one of which departed from London or Gravesend. The majority sailed to Auckland, although the numbers of birds arriving to South Island and North Island are similar (~330 vs 386; Figure 3). Details of individual ships are listed in Table 1.

Name	From	To	Departure	Arrival	Loaded	Survived	Note	Source
Flying Fish		Auckland	first half of 1859		NA	NA	Only information available is that yellowhammers were sent via her to Auckland	Stamford Mercury 12 August 1859, Page 3
Aloe	Gravesend	Auckland	5 th Feb 1863	7 th Jun 1863	NA	4	In total 112 birds loaded, among them 24 yellowhammers and chaffinches = no more than 23 yellowhammers loaded. Overall only 10% (12 birds) survived	Otago Witness 11 July 1863, Page 5; Daily Southern Cross 9 June 1863, Page 3
British Empire	Gravesend	Lyttelton	15 th May 1864	6 th Sep 1864	12	2	Private effort of Mr. Prince	Lyttelton Times 10 September 1864, Page 5; Press 7 September 1864, Page 2
Violet	London	Nelson	16 th Mar 1864	5 th Jun 1864	48	0 or 8	One article claim, that all had died, however, according to other 8 have arrived, which is more likely, as before the arrival of Violet no yellowhammers were present in the colony. The same holds for all-dying chaffinches.	Colonist 12 July 1864, Page 5; Nelson Examiner and New Zealand Chronicle 7 July 1864, Page 2
Novelty	London	Auckland	before 6 th Nov 1867	8 th Feb 1868	NA	4	However, 3 of them died after arrival	New Zealand Herald 10 February 1868, Page 3
Empress	Gravesend	Auckland	3 rd Dec 1867	28 th Mar 1868	NA	5	Information from reports. In total 400 birds loaded, 200 arriving.	Daily Southern Cross 14 March 1868, Page 4; Wellington Independent 19 March 1868, Page 4
Warrior Queen	London	Port Chalmers	21 th Oct 1867	28 th Jan 1868	12	8	Birds coming from Brighton area, released in Society's garden. Bills travelling with his son.	Daily Southern Cross 30 December 1867, Page 2; North Otago Times 4 February 1868, Page 2
Matoaka	London	Lyttelton	16 th Nov 1867	11^{h} Feb 1868	NA	1		Lyttelton Times 4 March 1868, Page 4
Blue Jacket	Gravesend	Lyttelton	7 th Aug 1868	30 th Oct 1868	NA	5		New Zealand Herald 28 November 1868, Page 6
Wild Duck	London	Wellington	1ª Oct 1868	5 th Jan 1869	NA	NA	Loaded 36 chaffinches and yellowhammers, 3 yellowhammers and 10 chaffinches sold on the market, should be total number, as almost all birds were sold.	Hawké's Bay Herald 12 January 1869, Page 3; Hawke's Bay Herald 23 January 1869, Page 3

Table 1. List of ships known to have been importing yellowhammers to New Zealand. In case that different numbers of arriving/departing birds are reported, those we consider more likely to be correct are in bold.

Name	From	To	Departure	Arrival	Loaded	Survived	Note	Source
City of Auckland	London	Auckland	19 th Oct 1870	29 th Jan 1870	NA	NA	40 birds in total, just 14 survived, some of them could be yellowhammers as the Society bought some before 9th March 1870	New Zealand Herald 2 February 1870, Page 3; Auckland Acclimatisation Society 1870
Inflexible	London	Auckland	22 nd Dec 1869	3 rd Apr 1870	24	10 or 18		New Zealand Herald 4 April 1870, Page 3; Wellington Independent 12 April 1870, Page 3
Mary Shepherd	London	Auckland	1ª Feb 1870	29 th May 1870	120	40 or 30		Daily Southern Cross 5 April 1870, Page 4; New Zealand Herald 30 May 1870, Page 3; Daily Southern Cross 30 May 1870, Page 3 (30)
Schiehallion	London	Auckland	23 th Feb 1870	$4^{ m th}$ Jun 1870	128 or 130	5	Claimed to be third shipment of yellowhammers, however wrongly (see above)	Auckland Star 7 June 1870, Page 2; Daily Southern Cross 7 June 1870, Page 3 (130); New Zealand Herald 6 July 1870, Page 6
Queen Bee	London	Auckland	22 th Oct 1870	8 th Feb 1871	140	NA	No information about its arrival	New Zealand Herald 10 January 1871, Page 2; Daily Southern Cross 6 February 1871, Page 3
Warrior Queen	London	Port Chalmers	$28^{\rm th} \operatorname{Nov} 1870$	25 th Feb 1871	50	31	Birds coming from Brighton area, released in Cavernsham	Colonist 4 April 1871, Page 4; Otago Daily Times 4 March 1871, Page 2
Caduceus	Gravesend	Auckland	16 th Dec 1870	23 rd Mar 1871	250	128 or 125	5 died after arrival. 120 (60 pairs) released in Domain	New Zealand Herald 6 April 1871, Page 2; Daily Southern Cross 4 April 1871, Page 3
Alexandrina	London	Auckland	5 th Feb 1871	$4^{\rm th}$ Jun 1871	250	NA	Experienced a heavy thunderstorm, however, it must brought at least 100birds. Liberated in Whangarei.	Daily Southern Cross 9 May 1871, Page 2
Countess of Kintore	London	Auckland	14 th Jun 1871	26 th Sep 1871	21	large quantity	Probably 19, that were liberated in Waiuku	New Zealand Herald 5 September 1871, Page 2; New Zealand Herald 27 September 1871, Page 2
City of Auckland	London	Auckland	10 th Sep 1871	10 th Dec 1871	70	20	Probably 18 of these liberated in Waikato	Grey River Argus 4 November 1871, Page 2; Daily Southern Cross 29 December 1871, Page 7

CaduceusLondonAuckland $18^{th} Oct 1871$ $2^{th} Feb 1872$ 70 48 Probably released in KaiparaNew ZealandCaduceusLondonPort $29^{th} Oct 1872$ $16^{th} Feb 1873$ NA100 $34 \sec to Lyttelton, fate of 66 unknownBruce Herald 2CharlotteLondonPort29^{th} Oct 187216^{th} Feb 1873NA10034 \sec to Lyttelton, fate of 66 unknownBruce Herald 2CharlotteLondonWellington16^{th} Nov 187216^{th} Feb 1873NA10034 \sec to Lyttelton, fate of 66 unknownBruce Herald 2CharlotteLondonUndon16^{th} Nov 187216^{th} Feb 1873NA10034 \sec to Lyttelton, fate of 66 unknownBruce Herald 2CharlotteLondonUndon10034 \sec to Lyttelton, fate of 66 unknownBruce Herald 2CharlotterPort29^{th} Nov 187216^{th} Feb 1873NA12034 \sec to Lyttelton, fate of 66 unknown27 \operatorname{Fars 4 Mat}HouseUndonUndon10034 \operatorname{terner Rangitira to Napier: in total 30020 \operatorname{March 18}32 \operatorname{March 18}34 \operatorname{sent} to 10034 \operatorname{sent} total 30020 \operatorname{March 18}HouseLondonIntel7^{th} Jan 18754^{th} May 187518012036 \operatorname{me} articles claim that only 160 or 17027 \operatorname{March 18}HouseLondonLondonLondon27^{th} May 187650 \operatorname{or 40}20 \operatorname{ont} eleased to wild - sent toNew Zealand 18WaimateLondonLondon<$	Name	From	To	Departure	Arrival	Loaded	Survived	Note	Source
Charlotte GladstonePort LondonPort PortPort Star 3 MCharlotte GladstoneLondonPort Chalmers 29^{th} Oct 1872 16^{th} Feb 1873NA100 34 sent to Lyttelton, fate of 66 unknownBruce Herald 2. Star 3 MForfarshire LondonLondonWellington 16^{th} Nov 1872 16^{th} Mar 1873NA12However, the birds were forwarded on out of 500 loaded birds died.Bruce Herald 2: Press 4 Mai 2.0 March 18;Tintern MbbyyLondonLyttelton 7^{th} Jan 1875 4^{th} May 1875 180 180 $500me$ articles claim that only 160 or 170Star 5 M Nor 1879Waimate LondonLytteltonZthelton 27^{th} Nov 1879 50 or 40 20 or 40 20 or 40 20 mearticles claim that only 160 or 170New Zealand H New Zealand HWaimateLondonLytteltonZthelton 20^{th} Nov 1879 50 or 40 20 or 40 20 mearticles claim that only 160 or 170New Zealand H New Zealand H	Caduceus	London	Auckland	18 th Oct 1871	2 th Feb 1872	70	48	Probably released in Kaipara	New Zealand Herald 12 December 1871, Page 3; Auckland Star 3 February 1872, Page 2
Forfarshire IbudonLondonWellington 16^{th} Nov 1872 2^{nd} Mar 1873NA12However, the birds were forwarded on steamer Rangitra to Napier. in toral 300Wanganui Hera 2. Press 4 Mai 2. March 18.Forfarshire IbudonLondonLyttelton 7^{th} Jan 1875 4^{th} May 1875 180 120 Mowever, the birds were forwarded on a total 300Wanganui Hera 	Charlotte Gladstone	London	Port Chalmers	29 th Oct 1872	16 th Feb 1873	NA	100	34 sent to Lyttelton, fate of 66 unknown	Bruce Herald 21 February 1873, Page 5; Star 3 March 1873, Page 2
Tintern AbbeyLondonLyttelton7 th Jan 18754 th May 1875180180Some articles claim that only 160 or 170Star 5 NAbbeyLondonLondon7 th Jan 18754 th May 1875180180180New Zealand FMainateLondonLondonLondon27 th Nov 18795 th Mar 188050 or 4022Birds not released to wild - sent to AustraliaPage 5; North 6	Forfarshire	London	Wellington	16 th Nov 1872	2 nd Mar 1873	NA	12	However, the birds were forwarded on steamer Rangitira to Napier. in total 300 out of 500 loaded birds died.	Wanganui Herald 19 March 1873, Page 2; Press 4 March 1873, Page 2; Press 20 March 1873, Page 2; Wellington Independent 3 March 1873, Page 2
WaimateLondonLyttelton 27^{th} Nov 1879 5^{th} Mar 188050 or 4022Birds not released to wild - sent toPage 5; North (1880, Page 2)	Tintern Abbey	London	Lyttelton	7 th Jan 1875	4 th May 1875	180	180	Some articles claim that only 160 or 170 were loaded, however, 180 arrived.	Star 5 May 1875, Page 2
	Waimate	London	Lyttelton	27 th Nov 1879	5 th Mar 1880	50 or 40	22	Birds not released to wild – sent to Australia	New Zealand Herald 16 January 1880, Page 5; North Otago Times 16 January 1880, Page 2 (40); Star 5 March 1880, Page 2

It is generally believed that data on bird survival during voyages on ships is lacking (Duncan et al. 2006). However, we can retrieve information of this sort from the digitised newspaper archives. For yellowhammers, we have complete data on the number of loaded birds, and the number of survivors, for 11 ships (Table 1). On average the survival rate for yellowhammers was about 50% (481-502 survivors out of 956-968 birds shipped). Some birds died before the ships departed (Daily Southern Cross 14 March 1868, Page 4) or in the first few days of the voyage (Otago Witness 11 July 1863, Page 5). The main sources of bird mortality were poor care due to the absence of an experienced bird keeper on board (Canterbury Acclimatisation Society 1870), suboptimal positioning of cages next to the galley, lack of food (Otago Witness 8 February 1868, Page 5), drowning when water reached the deck (Wellington Independent 8 February 1868, Page 4), disease caused by contaminated water (Otago Acclimatisation Society's Minutes; Otago Daily Times 4 March 1871, Page 2), and severe cold weather (Daily Southern Cross 11 February 1868, Page 4). In one reported case, mortality of waterfowl was ascribed to hungry passengers (Otago Daily Times 5 March 1873, Page 2). Some birds also escaped from their cages and were lost at sea (Otago Daily Times 4 March 1871, Page 2). Voyages with yellowhammers on board took on average 102 days, but varied from 80 to 122 days. However, there was no correlation between the duration of the voyage and the mortality rate of yellowhammers (r = 0.33, P = 0.29). We might expect higher mortality of birds coming from the Northern Hemisphere summer across the Tropics to the Southern Hemisphere winter, but the number of ships for which data are available is too low (n = 11) to test for the effect of departure season on mortality.

Attempts were also made to transport alien bird species as eggs, in the hope of reducing costs of transport. In 1862, Captain Francis Stevens imported a box of eggs of English birds coated with glycerine, which he offered to (and was accepted by) the Auckland Acclimatisation Society. He had undertaken this importation as an experiment to test whether birds could be transported as eggs, with the glycerine coating presumably to preserve the egg in a state of "suspended animation". Stevens suggested removing the glycerine just prior to putting the egg under an appropriate surrogate mother (Daily Southern Cross 27 October 1862, Page 3). The outcome of this experiment is not recorded, although it is predictable. This method of extending the viability of eggs was nevertheless also taken seriously five years later by the Canterbury (Canterbury Acclimatisation Society 1867) and Otago Acclimatisation Societies (Fifth Annual report of the Otago Acclimatisation Society extracted from Otago Acclimatisation Society's Minutes), and some 13 years later by an experimenter from Australia (New Zealand Herald 2 November 1880, Page 3). Various experiments have shown that, under certain conditions, eggs can be successfully hatched even several weeks after laying (Yoo and Wientjes 1991; Dudusula 2009; Gomez-de-Travecedo et al. 2014), and so the idea may not be so far-fetched. Nevertheless, the shortest voyage time to New Zealand at the time found by us (69 days for a ship transporting skylarks; New Zealand Herald 15 February 1866, Page 4) was still well above the maximum storage period in tests to date (42 days, Gomez-de-Travecedo et al. 2014).

Introduction into New Zealand

Data from newspapers, Acclimatisation Society records and other sources reveal that yellowhammers were imported to six regions of New Zealand: Auckland, Nelson, Canterbury, Otago, Hawke's Bay and Wellington (Table 2, Figure 1). The last two have been overlooked in previous studies (Thomson 1922; Wellwood 1968; Veltman et al. 1996; Duncan 1997).

Private efforts to introduce English birds happened before the first Acclimatisation Society was established in Auckland in 1861 (Daily Southern Cross 26 November 1861, Page 3). For example, in 1859, some yellowhammers were sent to Auckland on the ship Flying Fish (London Standard 4 August 1859). However, these haphazard trials were probably not successful (Daily Southern Cross 26 November 1861, Page 3). The Canterbury Acclimatisation Society also had a bad experience with uncoordinated importations of birds, as most of the birds died during the voyage (Canterbury Acclimatisation Society 1866), and as a result concentrated its later efforts on fewer shipments consisting of more birds (Canterbury Acclimatisation Society 1870). Richard Bills insisted that birds should be liberated in large numbers at one locality and be allowed to spread naturally. This attitude was later adopted by the Otago Acclimatisation Society (Otago Daily Times 23 June 1871, Page 2) and also by the Canterbury Acclimatisation Society, when Richard Bills took care of birds (Press 1 March 1872, Page 3; Press 1 March 1873, Page 2). When his son was in charge in 1875, the Canterbury Acclimatisation Society had very little control over where birds were eventually introduced as these were sold to subscribers and other applicants, though on condition that they would be liberated within the Canterbury region (Canterbury Acclimatisation Society's Minutes, Star 27 January 1875, Page 2). Similarly, Auckland Acclimatisation Society spread yellowhammers to more regions in 1871 (Figure 4).

According to Thomson (1922) yellowhammers were first introduced by the Nelson Acclimatisation Society in 1862. However, the first report of this Society, presented in September 1864 (Nelson Examiner and New Zealand Chronicle 12 September 1864, Page 2), makes it obvious that the first three yellowhammers were not liberated before 1863, and probably as late as 1864: the first known ship with yellowhammers on board, the Violet (Colonist 12 July 1864, Page 5), did not arrive into Nelson until June 1864. Broad (1892) and Thomson (1922) claim that, after that, the Society kept no records. That is not actually true (Nelson Evening Mail 2 May 1867, Page 2; Daily Southern Cross 1 May 1868, Page 4): rather, both Minutes and Letterbook of the Society from the period between 1863 and 1879 were destroyed in a fire (Sowman 1981). Fortunately, at least some information about the activities of the Society was preserved in newspapers. However, apart from the report from 1864, there is no information about yellowhammers from Nelson, and neither are they mentioned in an 1870 report on the English birds introduced by the Acclimatisation Society there (Star 18 November 1870, Page 2; Sowman 1981).

Thomson (1922) claimed that the Auckland Acclimatisation Society introduced eight yellowhammers as early as 1865, but at that time the Society barely existed, as it had

introduction and translocation events for yellowhammers to
introduction and translocation events for yellowhammers t
introduction and translocation events for yellowhar
introduction and translocation events for y
introduction and translocation events
introduction and translocation
introduction and
introduction
intro
F
list c
A
ч.
Ð
Р

Table 2	2. A list of inti	roduction an	ום ודמוזצוטכמנוטה בעכוו			
Year	Type	Region	Locality	Number	Note	Source
1863/4	Introduction	Nelson	NA	3		Nelson Examiner and New Zealand Chronicle 12 September 1864, Page 2
1865	Introduction	Auckland	NA	8	No confirmation either in reports or in Newspapers	Thomson (1922)
1868	Introduction	Auckland	NA	5	From Sciehallion	Thomson (1922), Auckland Acclimatisation Society 1869
1870	Introduction	Auckland	Auckland	14	According to reports, 16 were liberated (Auckland Acclimatisation Society 1870)	Daily Southern Cross 2 August 1870, Page 3
1871	Introduction	Auckland	Whangarei	100	Probably birds from Alexandrine	Daily Southern Cross 4 July 1871, Page 3; Daily Southern Cross 19 August 1871, Page 2
1871	Introduction	Auckland	Auckland	120	Birds from Caduceus	Auckland Acclimatisation Society 1872 (where), Daily Southern Cross 4 April 1871, Page 3 (how much)
1871	Introduction	Auckland	Waiuku	19	Probably birds from Countess of Kintore	Daily Southern Cross 3 October 1871, Page 2
1872	Introduction	Auckland	Waikato	18	Probably from City of Auckland	New Zealand Herald 10 January 1872, Page 3
1871/2	Introduction	Auckland	Kaipara	43+	The sum for 1871 is 300+, numbers known for other locations. Probably birds from Caduceus.	Auckland Acclimatisation Society 1872; Auckland Star 3 February 1872, Page 2
1872	Introduction?	Auckland	Matakohe	NA	Remainders from Caduceus?	New Zealand Herald 31 March 1873, Page 2
1876	Translocation	Auckland	NA	27	Gift to Sir George Grey	Daily Southern Cross 4 April 1876, Page 1
1876	Translocation	Auckland	Bay of Islands	18		New Zealand Herald 2 May 1876, Page 3
1876	Translocation	Auckland	Kawau	16		New Zealand Herald 20 June 1876, Page 3
1876	Translocation	Auckland	Kaipara / Hokianga	several		New Zealand Herald 2 May 1876, Page 3
1877	Translocation	Auckland	New Plymouth	28		Taranaki Herald 25 September 1877, Page 2
1869	Introduction?	Wellington	NA	3?	3 were sold. Were they released as well?	Hawke's Bay Herald 23 January 1869, Page 3; Evening Post 6 January 1869, Page 3
1873	Introduction	Hawke's Bay	districts around Napier	12 or 13	arrived on Forfarshire	Wanganui Herald 19 March 1873, Page 2; Evening Post 7 March 1873, Page 2; Press 20 March 1873, Page 2
1867	Introduction	Canterbury	Christchurch gardens	1		Lyttelton Times 7 January 1868, Page 2; Canterbury Acclimatisation Society 1867
1868	Intruduction	Canterbury	NA	5	arrived on ship Blue Jacket	Lyttelton Times 19 December 1868, Page 2

1873 Introducti	1873 Introducti	1875 Introducti	1875 Introducti	1868 Introducti	1871 Introducti	1876 Translocat	1876 Translocat	1879 Translocat	1879 Translocat
on Canterbury	on Canterbury	on Canterbury	on Canterbury	on Otago	on Otago	on Otago	on Otago	on Otago	on Otago
Christchurch (gardens)	Ilam	South Canterbury, within 50km from Timaru	North Canterbury	Dunedin	Caversham	Tapanui	Inch Clutha	Queenstown	Stewart Island
16	18	40	140	8	31	29 or less, possibly 14	9	24	32
	34 minus those liberated in Gardens	Part of those arriving by Tintern Abbey	The rest from 180 birds arriving by Tintern Abbey	arrived on Warrior Queen	arrived on Warrior Queen	caught in North East Valley, not confirmed in report	caught in North East Valley	probably released in Arrowtown	
Press 1 March 1873, Page 2	Star 3 March 1873, Page 2	Timaru Herald 2 June 1875, Page 3	Star 31 May 1875, Page 2; Figure 5	Otago Daily Times 14 February 1868, Page 4	Otago Acclimatisation Society's Minutes	Clutha Leader 30 March 1876, Page 5; Tuapeka Times 26 April 1876, Page 4	Otago Acclimatisation Society 1878; Star 22 February 1876, Page 3	Otago Acclimatisation Society's Minutes; Lake Wakatip Mail 26 July 1879, Page 2	Otago Acclimatisation Society's Minutes; Otago Daily Times 13 May 1879, Paze 3

_

_

lost its Secretary through his involvement in the Waikato Wars (New Zealand Herald 28 October 1865, Page 4). It is at least theoretically possible that those eight birds were descendants of vellowhammers arriving to Auckland on the Aloe in 1863 (Otago Witness 11 July 1863, Page 5). The Society was re-established in 1867 (and the reports are only available from that year on). Four birds claimed by Thomson (1922) to have been introduced in 1867 were actually not released, because three of them died after arrival (Auckland Acclimatisation Society 1868). In 1868, five yellowhammers arrived on board of the Empress (Daily Southern Cross 14 March 1868, Page 4, Auckland Acclimatisation Society 1869); however, it is not clear whether they were liberated. If they were, then it was probably directly to a garden of the Society (Daily Southern Cross 4 August 1868, Page 4; Auckland Acclimatisation Society 1869). In 1869, some yellowhammers were observed in Papatoetoe, 17 km from the Society's garden (Daily Southern Cross 4 May 1869, Page 6). It is possible that these could have been birds released the previous year (or their offspring). According to reports, 16 yellowhammers were imported in 1870 and liberated directly on the Society's grounds (Auckland Acclimatisation Society 1871), although the number of birds coming to Auckland harbour that year was at least 45 (Table 1).

The most important year for yellowhammer releases in the Auckland region was 1871, when more than 300 birds were liberated: 100 to Whangarei, 120 to Auckland, 43 or more to Kaipara, 19 to Waiuku and 18 to Waikato (Auckland Acclimatisation Society 1872; Daily Southern Cross 19 August 1871, Page 2; Daily Southern Cross 4 April 1871, Page 3; Daily Southern Cross 3 October 1871, Page 2; New Zealand Herald 10 January 1872, Page 3; Figure 4). In 1872, some birds were released in Matakohe (Auckland Acclimatisation Society 1873), probably remainders from previous shipments. In 1876, the Society hired a full-time bird catcher, whose duty was to catch birds for translocations, and two consignments of yellowhammers were translocated to Kawau and the Bay of Islands (Auckland Acclimatisation Society 1877), and one given to George Grey (Daily Southern Cross 4 April 1876, Page 1). Later on, another two consignments were sent to Australia (Evening News 30 September 1879, Page 3; Poverty Bay Herald 29 June 1880, Page 2) and one to New Plymouth for the Taranaki Acclimatisation Society (Taranaki Herald 25 September 1877, Page 2; Taranaki Herald 18 March 1878, Page 2).

In Otago, the Acclimatisation Society did not waste resources on introductions of yellowhammer. Eight yellowhammers were liberated in Dunedin in 1868 (Otago Acclimatisation Society's Minutes); in 1871, 31 were released in Cavernsham, now part of Dunedin (Otago Acclimatisation Society 1871; Otago Witness 11 March 1871, Page 5), where they were observed in large numbers three years later (Otago Daily Times 30 September 1874, Page 7). After 1871, all liberated birds appear to have been translocations from one part of Otago to another. There is still one uncertainty, though. In 1873, the Otago Acclimatisation Society helped Canterbury to transport birds from England (there was no ship going to Lyttelton from London soon enough, and so the birds were put on a ship to Otago). One hundred yellowhammers arrived into Port Chalmers (Wellington Independent 27 February 1873, Page 2), but only 34 were forwarded to Lyttelton (Star 3 March 1873, Page 2; Canterbury Acclimatisation Society's Letterbook, page 197). It is unclear what happened to the remaining 66 birds. They probably were



Figure 4. The number of imports and liberations of yellowhammers in the Auckland region in 1871 (likely scenario; see text for more details).

not liberated in Otago, as the Otago Acclimatisation Society kept careful records. They were not lost on the way either, as the re-shipment on the Phoebe from Dunedin to Christchuch arrived with scarcely any loss (Otago Daily Times 7 March 1873, Page 2), while the number of birds arriving to Lyttelton reported in newspapers is confirmed by a letter from the Honorary secretary of the Society (Canterbury Acclimatisation Society's Letterbook, page 197). Closer examination suggests that it is the number of birds arriving to Dunedin that is probably incorrect (Star 18 February 1873, Page 2; Press 19 February 1873, Page 2; Press 28 February 1873, Page 2; Otago Witness 1 March 1873, Page 12; Star 3 March 1873, Page 2; Press 4 March 1873, Page 2; Star 5 March 1873, Page 2; Timaru Herald 7 March 1873, Page 2; Otago Daily Times 12 March 1873, Page 6; Press 13 March 1873, Page 3; Canterbury Acclimatisation Society's Letterbook, pages 192–199). It may be that yellowhammers died after arrival due to the lack of water (Press 13 March 1873, Page 3) – the ship had to stay 2 days in quarantine because of the epidemic of typhoid fever (Canterbury Acclimatisation Society's Letterbook, page 197; Otago Daily Times 18 February 1873, Page 2).

Another doubt is cast by Chrisholm's (1907) statement that until 1870, there were not eight but 18 yellowhammers imported to Otago – however this is most likely a typographical error. In 1876, six yellowhammers were translocated from North East Valley to Inch Clutcha (Otago Acclimatisation Society 1878; Star 22 February 1876, Page 3). A further 40 were sent to Tapanui, but at least 11 of them died during the voyage due to poor conditions, as they all travelled in one box (Clutha Leader 30 March 1876, Page 5). Probably only 14 of them reached the final destination (Tuapeka Times 26 April 1876, Page 4). In 1879, 32 yellowhammers caught in Otago by Richard Bills' second son Charles were liberated on Stewart Island, and 24 in Queenstown (Otago Acclimatisation Society's Minutes; Otago Acclimatisation Society 1880).

As already noted, the Canterbury Acclimatisation Society has significant gaps in its reports and, without newspapers, it would appear they introduced only 35 birds. In fact, they actually introduced 219 or more. Moreover, two yellowhammers (out of 12 boarded) appear to have arrived in 1864, shortly after the Society started, thanks to the private efforts of a Mr. Prince (Lyttelton Times 10 September 1864, Page 5; Inverness Courier 27 April 1865). The first yellowhammer (a singleton) was released by the Canterbury Acclimatisation Society in 1867 (Canterbury Acclimatisation Society 1868; Lyttelton Times 4 February 1868, Page 3). In 1868, another one arrived on the Matoaka (Lyttelton Times 4 March 1868, Page 4), and later on, five arriving on the ship Blue Jacket were liberated, likely in Society's gardens (New Zealand Herald 28 November 1868, Page 6; Lyttelton Times 19 December 1868, Page 2). Even when added to the previous shipment of the pair by Mr. Prince, these are low numbers. Yet, flocks of yellowhammers were already being seen in the Society's garden in March 1870 (Press 2 March 1870, Page 2). Furthermore, in the Canterbury Acclimatisation Society Secretary's letter to the Taranaki Acclimatisation Society that same year, yellowhammers were mentioned on the list of successfully acclimatised bird species (Taranaki Herald 21 September 1870, Page 2). The following year, Hutton mentions Canterbury as a region, where yellowhammers had been introduced, in his Catalogue of New Zealand birds (Hutton 1871). Despite the successful establishment of yellowhammer, birds kept coming. In 1873, 34 yellowhammers were forwarded from Dunedin (see above) and released in Christchurch (Star 3 March 1873, Page 2). In 1875, 180 yellowhammers arrived on the Tintern Abbey (Press 4 May 1875, Page 2). Although there is no mention of the arrival of this ship or of the subsequent release of the birds in the Society's report, newspapers and the Society's minutes make it possible to reconstruct the fate of the birds to a certain degree. Forty were forwarded to South Canterbury and distributed as equally as possible among several localities within a distance of 50 km from Timaru (Star 15 May 1875, Page 2; Figure 5). Most of the remaining 140 birds were sold and released in various localities in North Canterbury, probably mainly in Christchurch and partly along the coast towards the South of Christchurch (Press 26 May 1875, Page 3; Star 31 May 1875, Page 2; Figure 5). That each location received at least three pairs was ensured by the fact that no one could buy fewer birds than that (Canterbury Acclimatisation Society's Minutes).

In 1880, the ship Waimate docked at Lyttleton, bringing a considerable number of birds that had not been requested, including 22 yellowhammers (Star 5 March 1880, Page 2). These birds were never released into the wild as the objections of local farmers



Figure 5. A map of possible localities of release of yellowhammers from the ship Tintern Abbey in 1875; red – localities selected for introduction in South Canterbury (40 in total), blue – home addresses of purchasers of yellowhammers in North Canterbury (140 in total).

were already too strong (Auckland Star 5 March 1880, Page 2). The Canterbury Acclimatisation Society had only two options – to destroy the birds, or to send them to another colony. They were sent to Adelaide in Australia (Press 27 March 1880, Page 3) and probably sold there (Canterbury Acclimatisation Society 1881).

The Wellington Acclimatisation Society never introduced yellowhammers. However, before this Society was formally recognised in 1871 (Wellington Independent 2 May 1871, Page 2), yellowhammers brought for acclimatisation purposes by the Provincial Government arrived on the ship Wild Duck in 1869 (Wellington Independent 16 January 1869, Page 6), and three of them were sold on the market (Hawke's Bay Herald 23 January 1869, Page 3). These were probably the only survivors of the transportation as all individuals of other species, for which the number of surviving individuals is known (New Zealand Herald 14 January 1869, Page 4), were sold (Wellington Independent 14 January 1869, Page 2) following the instruction of the Provincial Government (Evening Post 6 January 1869, Page 3). In 1875, an advertisement was circulated in the UK offering a reward for yellowhammers (Evening Post 17 July 1875, Page 2); this probably had no effect, as the Society did not spend any money on yellowhammers between 1871 and 1884, whereas transactions involving other bird species were noted (Wellington Acclimatisation Society's Cashbook for years 1871–1884; Figure 2). Yellowhammers are also not listed in the table of species introduced by the Wellington Acclimatisation Society between 1874 and 1884 (Wellington Acclimatisation Society 1887).

The Hawke's Bay Acclimatisation Society received 12 or 13 yellowhammers in 1873 from the ship Forfarshire, which were forwarded on the steam ship Rangitira (Wanganui Herald 19 March 1873, Page 2; Press 20 March 1873, Page 2). These were most likely released within 15 km of the city Napier (Evening Post 7 March 1873, Page 2; Press 20 March 1873, Page 2). The shipment was overseen by one of Richard Bills' sons (Press 4 March 1873, Page 2).

Establishment in the wild

The introduction of yellowhammers to New Zealand was rapidly successful. In 1871, when most of the yellowhammers introduced to the Auckland region had been released, the Acclimatisation Society was already claiming that the species was established and spreading. The Society even wrote to its agent in London, Grahame, not to send any more birds (New Zealand Herald 8 August 1871, Page 3). Yellowhammers were claimed to be acclimatised in the Canterbury region even earlier, in 1870 (Taranaki Herald 21 September 1870, Page 2), although shipments to there were not discontinued until 1880. Natural spread was enhanced by direct translocations, which were carried out in the Otago and Auckland regions (Table 2). By the 1900s, yellowhammers were established all over New Zealand (Figure 6), although the population close to Dunedin (Otago) almost perished for an unknown reason (Press 24 July 1897, Page 7; Otago Witness 21 September 1899, Page 62).

Environmental conditions in New Zealand would have been amenable to establishment. It is climatically similar to the UK. Large portions of the landscape were being cleared of forests even before the arrival of British colonists (McWethy et al. 2010), and were later transformed into cultivated habitats, fields or pastures (Wilmshurst et al. 1999), representing an ideal habitat for yellowhammers (del Hoyo et al. 2011).

Successful establishment in New Zealand was additionally supported by legislation. The Protection Act made any shooting of introduced small passerines illegal and fines were paid for violations (Nelson Examiner and New Zealand Chronicle 12 January 1864, Page 6; Daily Southern Cross 19 July 1866, Page 4; Protection of Animals Act 1867). The two native bird predators, New Zealand falcon (*Falco novaeseelandiae*) (Daily Southern Cross 5 December 1872, Page 2) and morepork (*Ninox novaeseelandiae*), were killed to stop them taking introduced birds (Daily Southern Cross 10 March 1870, Page 4), and even the native kingfisher (*Todiramphus sanctus*) was regarded as an enemy of introduced birds (Auckland Acclimatisation Society 1870). What difference this may have made in practice is unclear, as Europeans had introduced cats (Canterbury Acclimatisation Society 1867; New Zealand Herald 13 July 1878, Page 7) and ship rats (*Rattus rattus*), which attacked yellowhammers even on trees (New Zealand Herald 4 April 1871, Page 2), as well as a wide range of other alien mammalian predators (King 2005). Yellowhammers and other birds of English origin



Figure 6. A map of observation records of yellowhammers from the date of first introduction 1864 to 1900, based on reports from newspapers and from Drummond (1906).

would nevertheless presumably have been well adapted to the predation risk presented by these mammal species from their native range, as well as to bird predators due to the threat of the European sparrowhawk (*Accipiter nisus*).

Spread, public perception, and attempts at eradication

The first warning about the destructive behaviour of yellowhammers came as early as the mid-1860s (Lyttelton Times, 22 January 1866, Page 4), even before large-scale introductions had commenced. In the 1870s, the number of negative voices

increased as farmers started to experience direct consequences of yellowhammer establishment and spread (Auckland Star 31 August 1875, Page 2; New Zealand Herald 18 November 1876, Page 1; New Zealand Herald 11 July 1878, Page 3) – in total, negative references to yellowhammers appear twelve times in newspapers in the period 1872 to 1879. In early 1870's, the Canterbury Acclimatisation Society defended sparrows and regretted that farmers could not see the evident benefit from "insectivorous" birds brought for the fight against the ravages of insect pests (Canterbury Acclimatisation Society 1872–1874). Similarly, in 1877, farmers were decried as short-sighted by Mr. Firth, the president of the Auckland Acclimatisation Society, for their designation of these birds as feathered pests (New Zealand Herald 23 October 1877, Page 5).

By 1880, however, the tide had turned, and it was the intelligence and competence of the members of Acclimatisation Societies that was being questioned (Auckland Star 5 March 1880, Page 2). The "precious" load of birds being imported on the ship Waimate was the subject of criticism even before it had arrived, and given the abundance of the yellowhammer in New Zealand, was viewed as "carrying coals to Newcastle" in the eyes of one author (Star 26 January 1880, Page 4). Yellowhammers not only had to be forwarded on from the New Zealand territory, but were included for the first time, though not officially, on a list of granivorous birds (North Otago Times 13 March 1880, Page 2). From then on, they started to be killed in large numbers (New Zealand Herald 13 July 1880, Page 3) by various means: boys competed in egg collection (Bay of Plenty Times 4 December 1883, Page 2; Feilding Star 22 October 1898, Page 2), money was offered for their heads (Bay of Plenty Times 29 August 1882, Page 2) and poisoned grain was spread in winter fields (Waikato Times 14 July 1883, Page 2; Waikato Times 28 September 1889, Page 3). The public attitude towards yellowhammers was nicely expressed in a report from Parua Bay after the autumn harvest: "sparrows and yellowhammers will have to do a starve until sowing time comes" (New Zealand Herald 2 February 1889, Page 6).

In 1882, The Small Birds Nuisance Act came into force, which specified which means it was possible to use in the battle with birds injurious to crops, and under what conditions (www.nzlii.org/nz/legis/hist_act/sbna188246v1882n14275.pdf). Although yellowhammers are (unlike sparrows) not mentioned in the law, it is likely that it concerned them as it concerned all birds not protected as stated in other acts.

Some people continued to defend small birds into the 1880s and 1890s (New Zealand Herald 2 February 1884, Page 1), arguing that their temporary insectivory outweighed the damage to crops. In 1891, for example, an author calling himself "entomologist" speculated that the yellowhammer could be a useful and inexpensive weapon against codlin moth (*Cydia pomonella*), as it had proven to be in United States (Otago Witness 2 April 1891, Page 5). However, another writer questioned whether the U.S. yellowhammer is the same species as that in New Zealand (Nelson Evening Mail 11 February 1891, Page 3), which indeed it is not: 'yellowhammer' is an American vernacular name for the northern flicker (*Colaptes auratus*), a species of woodpecker. These voices of defence petered out in the 1890s, although in some locations the

yellowhammer was still argued to be a farmer's friend even into the twentieth century (Bay of Plenty Times 12 June 1901, Page 2).

In 1902, the yellowhammer was proclaimed an injurious bird under the Birds Nuisance Act, and the whole of the South Island was divided into eight parts to enhance coordinated efforts to tackle bird pests (New Zealand Herald 22 May 1903, Page 5; www. nzlii.org/nz/legis/hist_act/bna19022ev1902n25239). In 1905, Acclimatisation Societies introduced a bird predator, the little owl (*Athene noctua*), to help with these efforts, with no thought to its likely impact on already vanishing populations of native birds (Otago Acclimatisation Society Letterbook 1887-1914, page 220; Drummond 1912). Yellowhammers were still being killed in large numbers even in the late 1920s (Thomson 1926), and Oliver (1930) wrote that it must be ranked among the most harmful birds ever introduced to New Zealand. In some places it was considered to be more damaging than the sparrow (New Zealand Herald 17 May 1894, Page 6; New Zealand Herald 26 December 1904, Page 6). Nowadays, the yellowhammer is no longer regarded as a serious threat to New Zealand agriculture, although it is still listed as a crop pest there (Porter et al. 1994).

Although yellowhammers had attained the status of public enemy, some people were still willing to pay for them (Auckland Star 22 February 1888, Page 1; Auckland Star 26 August 1896, Page 1; Auckland Star 1 April 1910, Page 2). Among them was Charles Bills, son of Richard (Ashburton Guardian 18 October 1910, Page 3), who was probably interested in reselling the birds for profit. In 1911, yellowhammers were sold from Ashburton to a bird fancier in Dunedin (Ashburton Guardian 15 December 1911, Page 4), and the species was still being offered for sale as late as 1934 (Auckland Star 25 August 1934, Page 2). Thus, there existed a flow of birds across New Zealand even towards the middle of the twentieth century, the extent of which is difficult to assess.

Conclusions

Current biological invasions are the result of past human activities, and hence historical information potentially has a significant role to play in their study. The quality of New Zealand historical data on bird introductions has recently been criticised by Moulton et al. (2011, 2012a). They go so far as to state that "these historical records are in many cases mere rumors and impressions, and not actual "data" in any sense (Moulton et al. 2012a). We agree that the data presented by Thomson (1922) turn out on close inspection to contain inaccuracies, as clearly illustrated by our exploration of the historical records for the yellowhammer. Dates in Thomson (1922) are sometimes mismatched, there are significant omissions, all birds shipped are erroneously claimed to have been released and translocation is counted as introduction. Some later authors introduced further errors by misinterpreting the information (Williams 1969, Lever 2005). Nevertheless, it is far from the truth that historical data on bird introductions are poor. Our paper demonstrates that the quantity and quality of historical information may be much higher than has been argued, which can potentially improve

the precision of analyses based on it (Pyšek et al. 2015). Rather, they are simply hard work to unearth. That work has been made easier by the digitisation of key newspaper sources, but even so remains substantial. Focusing on just one species allowed us to mine the enormous seam of relevant primary sources as much as possible, and to assess the quality of records from Acclimatisation Societies and secondary compilations; it would be a Herculean task to assemble a faultless compilation of data for all species that the New Zealanders attempted to introduce (at least 120; Duncan et al. 2006).

Our exploration of the historical literature in fact reveals a wealth of information on bird introductions to New Zealand - indeed, far more is available, and in far more detail, than has hitherto been appreciated. Using it, we have been able to produce a detailed and nuanced history of the invasion of yellowhammer, tracking not only the transportation, introduction and establishment of the species, but also local attitudes to the species as it spread. Our study has significantly improved knowledge about the numbers, localities and dates of introductions, provided details about shipments, and filled in gaps and corrected misinterpretations in the literature. Assuming that the newspaper and Acclimatisation reports are reliable (and that the fact that different sources frequently confirm the same information suggests that they are), we have shown that Thomson (1922) underestimated introduction effort, whilst subsequent compilations (Andersen 1916, Williams 1969, Veltman et al. 1996; Duncan 1997) sometimes overestimated it. We have shown that the localities of release are often known, and that where they are not, it is often possible to identify likely sites. We have shown that it was common practice for birds to be liberated in large numbers at one locality and allowed to spread naturally. We have also found information about unorganised shipments, and shown that such birds represented a tiny fraction of the overall introduction effort for the yellowhammer.

We have also identified remaining gaps in our knowledge of yellowhammer introductions. Examples include the fate of the ship Queen Bee with 140 yellowhammers on board and the fate of the 66 birds arriving into Port Chalmers on the Charlotte Gladstone that were not forwarded to Lyttelton (Table 1). Nevertheless, these uncertainties are small relative to the body of information that is available. Despite them, it is clear that repeating our study on all the other bird species that New Zealanders attempted or succeeded in introducing would give an unparalleled database to study key features of the invasion process. Not least, it would put to bed ongoing arguments about the influence of propagule pressure on these species (Blackburn et al. 2013).

Although our study set out to understand the invasion history of the yellowhammer in New Zealand, our exploration of the historical literature also revealed snippets of information about the history of the yellowhammer in its native range. Nowadays, the yellowhammer is widespread and abundant in New Zealand, whereas in the UK it has experienced a rapid population decrease (Baillie et al. 2002). Recent studies have shown that it reaches three times higher densities in New Zealand than in similar habitats in its native range in the UK (MacLeod et al. 2005a, b). Historical sources show that the populations in the wild were already becoming scarcer in the UK around the time that birds were being shipped to New Zealand, partly due to the loss of habitat (typically hedges) and changes in agricultural land use (intensive harvesting), and partly because of "predation" pressure from humans, for food, population control of a perceived crop pest (Pall Mall Gazette 8 June 1872), or for use in the manufacture of fashionable objects (New Zealand Herald 11 March 1876, Page 1). Exploring the population history of a species from newspaper reports would until recently have been a lifetime's work, but the digitisation of archives is changing that. Our study suggests that the popular press, while not always very accurate in its reporting, may also represent a mine of information for studying changes in native bird populations that pre-date modern monitoring programmes. Indeed, data on acclimatisation represents only a tiny fraction of the information hidden in old newspapers, thus our study could even inspire research from other fields of study.

Acknowledgements

We thank the staff of the following institutions for their kind assistance: National Library of New Zealand in Wellington, Te Aka Matua Research Library (Museum of New Zealand/ Te Papa Tongarewa), Massey University Library in Palmerston North, Hocken's Archive in Dunedin, Christchurch City Libraries, Archives New Zealand/Te Rua Mahara o te Kāwanatanga – Christchurch Regional Office and British Library in London. Apart from that we thank Rosemary O'Neil from Christchurch City Libraries and Kate Guthrie from Hocken's Archive in Dunedin for scanning the letters of respective Acclimatisation Societies, Helen Pannett from Nelson Provincial Museum for providing access to research library after opening hours and kind assistance, Susan James for giving access to library of Forest&Bird office in Wellington, Paul Scoffield from Christchurch Museum for valuable advice and providing access to specimens of yellowhammers, Bernard Michaux from Auckland for pointing out the list of ships travelling to New Zealand. We thank Adam Petrusek and Lenka Krejčiříková for logistic support. We also thank two anonymous reviewers for useful comments. Last but not least we thank the late Vojtěch Jarošík for being always helpful and supportive, both to his student (Pavel) and colleagues (Petr, Tim). The study was funded by institutional resources of the Ministry of Education, Youth, and Sports of the Czech Republic, long-term research development project RVO 67985939 (Academy of Sciences of the Czech Republic) and Praemium Academiae award from the Academy of Sciences of the Czech Republic to P. P. and Grant Agency of the Charles University in Prague (project no. 312213).

References

- Andersen JC (1916) Jubilee History of South Canterbury. Whitcombe & Tombs limited, Auckland, 775 pp.
- Ashby CR (1967) The Centenary History of the Auckland Acclimatisation Society 1867–1967. Auckland Star Commercial Printers, Auckland, 143 pp.
- Auckland Acclimatisation Society (1868) Report of the Auckland Acclimatisation Society for the Year 1867–8. Daily Southern Cross office, Auckland.

- Auckland Acclimatisation Society (1869) Report of the Auckland Acclimatisation Society for the Year 1868–9. Daily Southern Cross office, Auckland.
- Auckland Acclimatisation Society (1870) Report of the Auckland Acclimatisation Society for the Year 1869–70. William Atkin, Auckland.
- Auckland Acclimatisation Society (1871) Report of the Auckland Acclimatisation Society Society for the Year Ending February 28, 1871. Herald Office, Auckland.
- Auckland Acclimatisation Society (1872) Report and Financial Statement of the Auckland Acclimatisation Society for the Year Ending February 29, 1872. Daily Southern Cross office, Auckland.
- Auckland Acclimatisation Society (1873) Report and Financial Statement of the Auckland Acclimatisation Society for the Year Ending February 28, 1873. William Atkin, Auckland.
- Auckland Acclimatisation Society (1876) Report and Financial Statement of the Auckland Acclimatisation Society for 1875–76. William Atkin, Auckland.
- Auckland Acclimatisation Society (1877) Report and Financial statement of the Auckland Acclimatisation Society for 1876–77. William Atkin, Auckland.
- Baillie SR, Crick HQP, Balmer DE, Beaven LP, Downie IS, Freeman SN, Leech DI, Marchant JH, Noble DG, Simpkin AP, Thewlis RM, Wernham CV (2002) Breeding Birds in the Wider Countryside: Their Conservation Status 2001. BTO Research Report 278.
- Blackburn TM, Lockwood JL, Cassey P (2009) Avian Invasions: the Ecology and Evolution of Exotic Birds. Oxford University Press, Oxford, 320 pp. doi: 10.1093/icb/icq059
- Blackburn TM, Prowse TAA, Lockwood JL, Cassey P (2011a) Passerine introductions to New Zealand support a positive effect of propagule pressure on establishment success. Biodiversity & Conservation 20: 2189–2199. doi: 10.1007/s10531-011-0081-5
- Blackburn TM, Prowse TAA, Lockwood JL, Cassey P (2013) Propagule pressure as a driver of establishment success in deliberately introduced exotic species: fact or artefact? Biological Invasions 15: 1459–1469. doi: 10.1007/s10530-013-0451-x
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011b) A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339. doi: 10.1016/j.tree.2011.03.023
- Broad L (1892) The Jubilee History of Nelson: from 1842 to 1892. Bond, Finney, Nelson.
- Brook BW (2004) Australasian bird invasions: accidents of history? Ornithological Science 3: 33–42. doi: 10.2326/osj.3.33
- Canterbury Acclimatisation Society (1866) The Second Annual Report of the Canterbury Acclimatisation Society. Christchurch.
- Canterbury Acclimatisation Society (1867) The Third Annual Report of the Canterbury Acclimatisation Society. Printed at the "Press" office, Christchurch.
- Canterbury Acclimatisation Society (1868) The Fourth Annual Report of the Canterbury Acclimatisation Society. Ward and Breves, Printers, Christchurch.
- Canterbury Acclimatisation Society (1870) The Fifth and Sixth Annual Report of the Canterbury Acclimatisation Society. Printed at the "Press" office, Christchurch.
- Canterbury Acclimatisation Society (1872) The Eigth Annual Report of the Canterbury Acclimatisation Society. Christchurch.
- Canterbury Acclimatisation Society (1873) The Nineth Annual Report of the Canterbury Acclimatisation Society. Printed at the "Times" office, Christchurch.

- Canterbury Acclimatisation Society (1874) The Tenth Annual Report of the Canterbury Acclimatisation Society. Printed at the "Times" office, Christchurch.
- Canterbury Acclimatisation Society (1877) The Twelfth and Thirteenth Annual Reports of the Canterbury Acclimatisation Society. Printed at the "Times" office, Christchurch.
- Canterbury Acclimatisation Society (1881) The Seventieth Annual Report of the Canterbury Acclimatisation Society. Printed at the "Press" office, Christchurch.
- Cassey P (2001) Determining variation in the success of New Zealand land birds. Global Ecology and Biogeography 10: 161–172. doi: 10.1046/j.1466-822x.2001.00224.x
- Chrisholm R (1907) Work of Acclimatisation: Particulars Regarding the Otago Society. Daily Times Print, Dunedin.
- Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89: 1541–1553. doi: 10.1890/07-0682.1
- Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023–1037. doi: 10.1007/s10530-005-3735-y
- D'Antonio CM, Levine J, Thomsen M (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. Journal of Mediterranean Ecology 2: 233–245.
- Daehler CC (2006) Invasibility of tropical islands by introduced plants: partitioning the role of isolation and propagule pressure. Preslia 78: 389–404.
- Dawson JC (1984) A Statistical Analysis of Species Characteristics Affecting the Success of Bird Introductions. BSc thesis, University of York.
- Del Hoyo J, Elliot A, Sargatal J (2011) Handbook of the Birds of the World. Volume 6: Mousebirds to Hornbills. Lynx Edicions, Barcelona, 589 pp.
- Dudusula IO (2009) Effects of storage methods and length of storage on some quality parameters of Japanese quail eggs. Tropicultura 27: 45–48.
- Duggan IC, Rixon CAM, MacIsaac HJ (2006) Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. Biological Invasions 8: 377–382. doi: 10.1007/s10530-004-2310-2
- Duncan RP (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. American Naturalist 149: 903–915. doi: 10.1086/286029
- Duncan RP, Blackburn TM (2002) Morphological over-dispersion in game birds (Aves: Galliformes) successfully introduced to New Zealand was not caused by interspecific competition. Evolutionary Ecology Research 4: 551–561.
- Duncan RP, Blackburn TM, Cassey P (2006) Factors affecting the release, establishment and spread of introduced birds in New Zealand. In: Allen RB, Lee WG (Eds) Biological Invasions in New Zealand. Springer-Verlag, Berlin, 138–154. doi: 10.1007/3-540-30023-6_9
- Druett J (1983) Exotic Intruders: the Introduction of Plants and Animals into New Zealand. Heinemann, Auckland, 291 pp.
- Drummond J (1906) Dates on which introduced birds have been liberated, or have appeared, in different districts of New Zealand. Transactions and Proceedings of the Royal Society of New Zealand 39: 503–508.

Drummond J (1912) Introduced birds of New Zealand. Condor 14: 227. doi: 10.2307/1362161

- Gomez-de-Travecedo P, Caravaca FP, Caravaca P (2014) Effects of storage temperature and length of the storage period on hatchability and performance of red-legged partridge (*Alectoris rufa*) eggs. Poultry Science 93: 747–754. doi: 10.3382/ps.2013-03329
- Green RE (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology 66: 25–35. doi: 10.2307/5961
- Haemig PD (2014) Aztec introduction of the great-tailed grackle in ancient Mesoamerica: Formal defense of the Sahaguntine historical account. NeoBiota 22: 59–75. doi: 10.3897/ neobiota.22.6791
- Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? Biological Invasions 10: 483–506. doi: 10.1007/s10530-007-9146-5
- Hutton FW (1871) Catalogue of the Birds of New Zealand with Diagnoses of the Species. J. Hughes, Wellington, 108 pp.
- King CM (2005) The Handbook of New Zealand Mammals. Oxford University Press, Oxford, 612 pp.
- Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasions by woody species in a temperate region. Conservation Biology 20: 1487–1498. Doi: 10.1111/j.1523-1739.2006.00477.x
- Lamb RC (1964) Birds, Beasts & Fishes: the First Hundred Years of the North Canterbury Acclimatisation Society. North Canterbury Acclimatisation Society, Christchurch.
- Lever C (2005) Naturalised Birds of the World. Christopher Helm Ornithology, London, 304 pp.
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20: 223–228. doi: 10.1016/j.tree.2005.02.004
- Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions 15: 904–910. doi: 10.1111/j.1472-4642.2009.00594.x
- Long JL (1981) Introduced Birds of the World. David & Charles, London, 528 pp.
- Macleod CJ, Duncan RP, Parish DMB, Wratten SD, Hubbard SF (2005a) Can increased niche opportunities and release from enemies explain the success of introduced yellowhammer populations in New Zealand? Ibis 147: 598–607. doi: 10.1111/j.1474-919X.2005.00445.x
- Macleod CJ, Parish DMB, Duncan RP, Wratten SD, Hubbard SF (2005b) Do yellowhammers *Emberiza citrinella* achieve higher breeding productivity in their introduced range than in their native range? Capsule success in New Zealand is not from enhanced reproductive productivity, but may be from better winter food supplies and fewer natural predators. Bird Study 52: 217–220. doi: 10.1080/00063650509461394
- McDowall RM (1994) Gamekeepers for the Nation: the Story of New Zealand's Acclimatisation Societies, 1861–1990. Canterbury University Press, Christchurch, 508 pp.
- McWethy DB, Whitlock C, Wilmshurst JM, McGlone MS, Fromont M, Li X, Dieffenbacher-Krall A, Hobbs WO, Fritz SC, Cook ER (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proceedings of the National Academy of Sciences of the USA 107: 21343–21348. doi: 10.1073/ pnas.1011801107

- Møller AP, Cassey P (2004) On the relationship between T-cell mediated immunity in bird species and the establishment success of introduced populations. Journal of Animal Ecology 73: 1035–1042. doi: 10.1111/j.0021-8790.2004.00879.x
- Moulton MP, Crooper WP Jr, Avery ML (2011) A reassessment of the role of propagule pressure in influencing fates of passerine introductions to New Zealand. Biodiversity & Conservation 20: 607–623. doi: 10.1007/s10531-010-9969-8
- Moulton MP, Cropper WP Jr, Avery ML (2012a) Historical records of passerine introductions to New Zealand fail to support the propagule pressure hypothesis. Biodiversity & Conservation 21: 297–307. doi: 10.1007/s10531-011-0165-2
- Moulton MP, Cropper WP Jr, Moulton LE, Avery ML, Peacock D (2012b) A reassessment of historical records of avian introductions to Australia: no case for propagule pressure. Biodiversity & Conservation 21: 155–174. doi: 10.1007/s10531-011-0173-2
- Oliver WRB (1930) New Zealand Birds. Fine Arts Ltd., Wellington, 209 pp.
- Otago Acclimatisation Society (1865) The First Annual Report of the Otago Acclimatisation Society. Henry Wise Printer, Dunedin.
- Otago Acclimatisation Society (1867) The Third Annual Report of the Otago Acclimatisation Society. Henry Wise Printer, Dunedin.
- Otago Acclimatisation Society (1871) The Seventh Annual Report of the Otago Acclimatisation Society. Printed at the "Daly Times" office, Dunedin.
- Otago Acclimatisation Society (1878) The Report of the Otago Acclimatisation Society for the Years 1876 and 1877. Printed at the "Daily Times" office, Dunedin.
- Otago Acclimatisation Society (1880) The Report of the Otago Acclimatisation Society for the Year Ending Dec. 31, 1879. Printed Mackay, Bracken & Co., Dunedin.
- Porter RER, Rudge MR, McLennan JA (1994) Birds and Small Mammals: a Pest Control Manual. Manaaki Whenua Press, Lincoln, 88 pp.
- Pyšek P, Manceur A, Alba C, McGregor K, Pergl J, Štajerová K, Chytrý M, Danihelka J, Kartesz J, Klimešová J, Lučanová M, Moravcová L, Nishino M, Sádlo J, Suda J, Tichý L, Kühn I (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology. doi: 10.1890/14-1005.1 [in press]
- Santos ESA (2012) Discovery of previously unknown historical records on the introduction of dunnocks (*Prunella modularis*) into Otago, New Zealand during the 19th century. Notornis 59: 79–81
- Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 40: 81–102. doi: 10.1146/annurev.ecolsys.110308.120304
- Sol D, Lefebvre L (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90: 599–605. doi: 10.1034/j.1600-0706.2000.900317.x
- Sowman W (1981) Meadow, Mountain, Forest and Stream: the Provincial History of the Nelson Acclimatisation Society, 1863–1968. Nelson Acclimatisation Society, Nelson.
- Stephens H (1851) On the birds destructive to the grain crops. In: The Book of the Farm. William Blackwood and Sons, Edinburgh, 377–384.
- Sullivan WA (1998) Changing the Face of Eden: a History of Auckland Acclimatisation Societies, 1861–1990. Auckland/Waikato Fish & Game Council.

- Taylor R (1868) The Past and Present of New Zealand: with its Prospects for the Future. Henry Ireson Jones, Wanganui.
- Thomson GM (1922) The Naturalisation of Animals and Plants in New Zealand. Cambridge University Press, Cambridge, 628 pp. doi: 10.5962/bhl.title.28093
- Thomson GM (1926) Wildlife in New Zealand. Part II. Introduced Birds and Fishes. New Zealand Board of Science and Art, Manual No.5. Government Printer, Wellington.
- Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. American Naturalist 147: 542–557. doi: 10.1086/285865
- Von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86: 3212–3218. doi: 10.1890/05-0427
- Wellington Acclimatisation Society (1887) Annual Report of the Wellington Acclimatisation Society for the Year Ending 31st August 1887. New Zealand Times, Wellington.
- Wellwood JM (1968) Hawke's Bay Acclimatisation Society Centenary 1868–1968. Hawke's Bay Acclimatisation Society, Hastings.
- Williams GR (1969) Introduced birds. In: Knox GA (Ed.) The Natural History of Canterbury. Reed, Wellington, 435–451.
- Wilmshurst JM, Eden DN, Froggatt PC (1999) Late Holocene forest disturbance in Gisborne, New Zealand: a comparison of terrestrial and marine pollen records. New Zealand Journal of Botany 37: 523–540. doi: 10.1080/0028825X.1999.9512651

Wilson E (1875) Acclimatisation. Unwin Brothers, London.

- Wonham MJ, Byers JE, Grosholz ED, Leung B (2013) Modeling the relationship between propagule pressure and invasion risk to inform policy and management. Ecological Applications 23: 1691–1706. doi: 10.1890/12-1985.1
- Yoo BH, Wientjes E (1991) Rate of decline in hatchability with preincubation storage of chicken eggs depends on genetic strain. British Poultry Science 32: 733–740. doi: 10.1080/00071669108417399

RESEARCH ARTICLE



Modeling the distribution of Norway rats (*Rattus norvegicus*) on offshore islands in the Falkland Islands

Michael A. Tabak¹, Sally Poncet², Ken Passfield², Carlos Martinez del Rio^{1,3}

 Program in Ecology, Department of Zoology & Physiology, University of Wyoming, 1000 E. University Ave. Laramie, WY 82071, USA 2 Beaver Island LandCare, PO Box 756 Stanley, Falkland Islands FIQQ IZZ
 Berry Biodiversity Institute, University of Wyoming, 1000 E. University Ave. Laramie, WY 82071, USA

Corresponding author: Michael A. Tabak (mtabak@uwyo.edu)

Academic editor: Daniel Sol | Received 18 August 2014 | Accepted 13 November 2014 | Published 16 January 2015

Citation: Tabak MA, Poncet S, Passfield K, Martinez del Rio C (2015) Modeling the distribution of Norway rats (Rattus norvegicus) on offshore islands in the Falkland Islands. NeoBiota 24: 33–48. doi: 10.3897/neobiota.24.8433

Abstract

Non-native rats (Rattus spp.) threaten native island species worldwide. Efforts to eradicate them from islands have increased in frequency and become more ambitious in recent years. However, the long-term success of some eradication efforts has been compromised by the ability of rats, particularly Norway rats (Rattus norvegicus) which are good swimmers, to recolonize islands following eradications. In the Falkland Islands, an archipelago in the South Atlantic Ocean, the distance of 250 m between islands (once suggested as the minimum separation distance for an effective barrier to recolonization) has shown to be insufficient. Norway rats are present on about half of the 503 islands in the Falklands. Bird diversity is lower on islands with rats and two vulnerable passerine species, Troglodytes cobbi (the only endemic Falkland Islands passerine) and *Cinclodes antarcticus*, have greatly reduced abundances and/or are absent on islands with rats. We used logistic regression models to investigate the potential factors that may determine the presence of Norway rats on 158 islands in the Falkland Islands. Our models included island area, distance to the nearest rat-infested island, island location, and the history of island use by humans as driving variables. Models best supported by data included only distance to the nearest potential source of rats and island area, but the relative magnitude of the effect of distance and area on the presence of rats varied depending on whether islands were in the eastern or western sector of the archipelago. The human use of an island was not a significant parameter in any models. A very large fraction (72%) of islands within 500 m of the nearest potential rat source had rats, but 97% of islands farther than 1,000 m away from potential rat sources were free of rats.

Keywords

Invasive species; eradication; Rattus norvegicus; metapopulation

Copyright Michael A. Tabak et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Introduced species can have detrimental consequences for native island communities (Wiles et al. 2003, Kurle et al. 2008) and rats are among the most problematic species introduced to islands (Hilton and Cuthbert 2010). Three species of rats (Rattus norvegicus, R. rattus, and R. exulans) live as commensals of humans. As a result of humanaided dispersal (Blackburn et al. 2004), these rodents are found on a very large fraction of the world's islands (King 1985) where they often have negative consequences for native species (Atkinson 1985). Rats can cause population declines and even the extinction of many species of island birds, amphibians, and reptiles (Towns et al. 2006, Cree et al. 1985). Eradicating rats from islands can lead to the recovery of native species and many of the ecological processes that they mediate. For example, between 12 and 22 years after rats were removed from several islands in New Zealand, population densities of seabirds recovered and their increase was accompanied by gains in soil nitrogen content (Jones 2010). Rats disperse to islands with human assistance, but they can also move among islands by themselves (Russell et al. 2010, Russell and Clout 2004). Norway rats (R. norvegicus) are particularly good swimmers and can reinvade eradicated islands (Russell et al. 2008). To eradicate rats successfully and permanently, it is necessary to understand the factors that determine their capacity to colonize islands (Fewster et al. 2011).

Norway rats (Rattus norvegicus) were introduced to the Falkland Islands (or "Falklands") in the 18th century (Poncet et al. 2011). They are present on the two largest islands, East and West Falkland, and about 235 of 503 smaller offshore islands that comprise the archipelago (Falkland Islands Government 2013). The Falkland Islands are situated in the southwest South Atlantic Ocean between latitudes of 51°S and 53°S and 57°30'W and 61°30'W. They occupy 12,173 km² of land and in 2012 had a human population of 2,932 inhabitants (Falkland Islands Government 2012). In addition to the introduction of Norway rats (henceforth referred to as "rats"), the Falklands have undergone significant ecological changes since the 18th century. These ecological changes include overgrazing with concomitant vegetation changes (McAdam 1980), increased fire frequency (Armstrong 1994, Woods and Woods 2006), climate change (Bokhorst et al. 2007), and declines in the abundance of marine mammals and seabirds throughout the archipelago (Palomares et al. 2006, Strange 1992). The pattern of human movement and activity on the islands has also varied since the arrival of sealers and whalers in the early 18th century and the establishment of the first permanent settlements in the 1760s (Strange 1992). Many, if not all, of these factors have likely influenced the distribution of rats.

The presence of rats in the Falkland Islands is associated with a significant reduction in the diversity and abundance of passerine birds (Hall et al. 2002, Tabak et al. 2014). Two species of passerines are particularly sensitive to rats. Cobb's wren (*Troglodytes cobbi*, Fig. 1), the only endemic land bird species of the Falklands, is absent from islands in



Figure 1. Two bird species of conservation concern in the Falkland Islands. Cobb's wren (**A**) and Tussacbird (**B**) are both highly vulnerable to the presence of rats. Protecting these species from local extinction requires effective management in the Falkland Islands, including the eradication of Norway rats.

which rats are present. Cobb's wren is considered a vulnerable species by the International Union for the Conservation of Nature (IUCN 2012). Tussacbird (*Cinclodes antarcticus*, Fig. 1) is found very rarely on islands with rats and, when they are present, their abundance is much lower than that observed on islands free of rats (Tabak et al. 2014). This species is only found in the Falkland Islands and on rat-free islands of the southern tip of South America (Strange 1992, Pina and Cifuentes 2004). Protection of these two species requires the maintenance of rat free islands in the Falkland Islands. Rat eradications appear to benefit the diversity of native passerine birds in the Falklands (Tabak et al. 2014a), but eradication efforts are hampered by the ability of rats to swim between islands.

Brown (2001) suggested that if an island in the Falkland Islands was at least 250 m (later revised to 350 m) from the nearest rat-infested island, it was likely to be safe to eradicate rats from this island because rats would not reinvade by swimming. These threshold distances were derived from physiological experiments on the maximum swimming distance of rats at different temperatures. Sea surface water temperature in the Falklands ranges from 5 to 8 °C (Waluda et al. 1999; Agnew et al. 2000). The length of time that Norway rats can survive in water decreases with temperature. At 9 °C, this time is about 9 \pm 1 min (Le Blanc 1958). The maximum speed Norway rats have been recorded swimming in the laboratory is 1.4 km/h (Dagg and Windsor 1972). Therefore, assuming that Norway rats can survive in Falkland Islands seawater for ten minutes and that they swim their maximum speed this entire time, their estimated maximum swim distance is 233 m. The estimates of 250 to 350 m were conservative based on laboratory studies.

Since 2001, 66 islands in the Falklands have been successfully treated for rat eradication. However, rats have reinvaded 10 of the islands from which they were eradicated (Falkland Islands Government 2013; Fig. 2), suggesting that this threshold distance for preventing reinvasions is too low. Tabak et al. (2014b) used population genetic



Figure 2. Evidence for rat reinvasion following eradication. Gnawed chewsticks (**A**, right) and rat tracks (**B**) indicate that an island has been reinvaded by rats. Chewsticks are wood pieces soaked in edible oil. They are useful and cost-effective tools used to determine if an eradication attempt was effective at removing rats and to determine if rats have returned to an island after a successful eradication.

analyses to estimate how far rats tend to move between islands in the Falkland Islands. They found evidence of significant migration, and hence presumably rats swimming, distances of up to 830 m. They suggested that 830–1,000 m was a conservative distance for safe and effective eradication. Our study complements the work of Tabak et al. (2014b) by our use of occupancy modeling based on the distribution of rats and the distance to the nearest rat source to estimate the maximum swimming distance of rats between islands.

Here we examined the relationship between the presence of Norway rats and island characteristics in the Falkland Islands. To guide our analyses, we conceived of rats in the Falklands as a metapopulation in which island sub-populations are linked by dispersal, and in which the presence of rats is determined by the balance between colonization and extinction among islands (Fronhoffer et al. 2012). Following this classical view of metapopulations (Levins 1969, 1970), we hypothesized that the presence of rats would decrease with distance from the nearest island with rats, the island presumably functioning as a reservoir and source of rats (for the purposes of this manuscript, we use "source" to describe any island on which rats are present). We also hypothesized that rats would be found more often on larger than on smaller islands (Hanski et al. 1996). Larger islands are more likely to be visited by humans, represent a larger colonization target, and presumably maintain larger rat populations that are less likely to become locally extinct than smaller islands (Russell and Clout 2004). In addition to these two major variables, we examined the potential roles of geographic location and human presence on the prevalence of rats on islands, as humans tend to carry rats when they travel to islands (Atkinson 1985).

Methods

Our analysis included 158 islands, 56 of which had rats and 102 of which had no evidence of rats (Fig. 3). None of the islands in this analysis had been the subject of eradication programs. Islands ranged in size from 0.3 ha to 5,585 ha. Data for rat status (presence or absence) on each island, island surface area, and the geographic location of each island (east or west sector of the archipelago) were obtained from the Falkland Islands Biodiversity Database (Falkland Islands Government 2013). Surveyors walked at least 1 km along the coast and assessed the presence of rats based on fresh sign (i.e., droppings, tracks, sightings of live animals, and rats caught in traps). It is possible that rats were present on some islands, but not detected in surveys (Mackenzie et al. 2002). Therefore, we estimated the detection probability of rats by conducting 5 repeated surveys on each of 10 randomly selected islands in the Falkland Islands from 30 March–27 April 2013.

Data for human activity on each island were obtained from the Falkland Islands Biodiversity Database (Falkland Islands Government 2013). Human use is defined as the use (both historical and contemporary) of an island by humans for activities involving temporary or permanent occupation of the island and landing of livestock, building materials, and other goods. Most of these activities in the Falkland Islands are traditionally associated with grazing of livestock. We ranked the intensity of human use into 5 categories according to the type of occupation or use: 0 (island has never had grazing nor structures and there has never been temporary nor permanent human occupation or use); 1 (island has been grazed but no structures have been built and the island has no history of temporary nor permanent occupation by humans); 2 (island has been grazed and minor structures [i.e., fences or corrals but not woolsheds, huts, or houses] have been built and there has never been temporary nor permanent human occupation); 3 (island has been grazed, minor structures and major structures [i.e., woolsheds, huts, or houses] have been built, and the island has been occupied temporarily but never year round); and 4 (island has been grazed, minor and major structures have been built, and the island has been occupied year round).

To determine if island location had an effect on the probability of rat occupancy, we allocated islands to one of two geographical sectors: western or eastern. We separated the islands into sectors by measuring the straight-line distance between each island (i) and East Falkland (e) and West Falkland (w) using maps published by the Directorate of Overseas Surveys (1961) with a resolution of 1:50,000. If the distance from island *i* to East Falkland (D_{ie}) was less than the distance to West Falkland (D_{ie}) , we assigned this island to the eastern sector. If $D_{iw} < D_{ie}$, we assigned island *i* to the western sector. For each island, we identified the nearest rat source (or potential source) by measuring the straight-line distance from each island (i) to the nearest rat-infested island (j) and the second-nearest rat infested island (k) using maps published by the Directorate of Overseas Surveys (1961) with a resolution of 1:50,000.

To identify the most important variables that predict rat distribution in the Falkland Islands, we constructed a collection of nested generalized linear models (GLMs) using



Figure 3. Distribution map of Norway rats in the Falkland Islands. Islands with rats (red points) appear in clusters. We hypothesize that rats are able to move between islands that are geographically close. Islands without rats (blue points) are typically farther from the mainland (East and West Falkland). Islands were assigned to geographic sectors based on their location: islands closer to West Falkland are in the western sector, while islands closer to East Falkland are in the eastern sector.

rat presence or absence as response variables. The full and most complex model included as independent variables the following four factors: log,-transformed distance to the nearest rat-infested island (Log, Dist), log10-transformed island area (Log10A), human use (HumUse), and geographic sector (eastern or western; West). Because island area ranged from 1 to over 5,000 ha, we log-transformed data using base 10. This transformation allowed us also to compare graphically with data on other islands and in other publications (log₁₀ is traditionally used in island biogeography studies; MacArthur and Wilson 1967; Morley and Winder 2013). We used a base 2 logarithmic transformation for distances as it allowed easier visualization of the shorter distances that we wanted to emphasize for comparison with the estimated maximal distance that rats were supposed to swim (i.e., less than 500 m). The full model also included all possible pairwise interactions between these predictor variables. We compared these models using AIC_c scores and chose the model with the lowest score as the model best supported by data. For each of the models we fitted in the analyses, we estimated Nagelkerke's pseudo-R² (N-R²) as a qualitative measure of goodness of fit (Nagelkerke 1991). For each of these models we also tested for overdispersion (d > 1; Moore 1986). When multiple models had similar levels of support $(\Delta AIC_{c} < 2)$ we calculated predicted values associated with each of the alternative models (Anderson 2008). Because we favor parsimony in our models, if the differences between predicted values were very small and models had similar levels of support ($\Delta AIC_c < 2$) we chose the simpler of models (i.e., the model with fewer variables; Burnham and Anderson 2002). Our models do not consider the potential role of shipwrecks in dispersing rats because data on the history of shipwrecks are not available for each island. However, 13 of the 158 islands analyzed are known to have shipwrecks off their shore (Southby-Tailyour 1985). Of these, only 3 islands are rat infested.

Results

We found that rats were present on 5 of the 10 islands that were surveyed repeatedly. On islands where rats or their sign were found to be present, rats (or their sign) were detected in each of the 5 repeated surveys. They were not found in any repeated surveys of islands determined to be rat-free. Therefore, the detection probability of rats in the Falkland Islands can be assumed to be close to 100%.

The model best supported by the data included an effect of distance to the nearest rat-infested island, island area, and geographical sector (Table 1). The probability of rat occupancy decreased with distance to the nearest rat source, increased with island area, and was higher in the western sector. The overdispersion parameter was not significant for this model (p = 0.95). None of the models that were best supported by the data included human use ($\Delta AIC_{c} > 2$). Since there was a significant effect of the geographical sector in the model, we separated the islands into two sectors (eastern and western sectors) and ran the models separately for each of them. When we analyzed the data separately for each geographical sector, in all of the best-supported models, rat occupancy decreased with distance to the nearest rat-infested island (Tables 2 and 3). In the western sector, two models had substantial support (ΔAIC_{c} < 2, Table 2). These models both included distance to the nearest rat source and island area as effects, but one included an interaction between these variables, while the other did not. We calculated the difference between the predicted values associated with these models. Because the mean difference in the values predicted by the two alternative models was very small $(0.0022 \pm 0.083 \text{ (SD)})$, we chose the simpler of the two models. This model included an effect of the log of island area as well as the log of the distance to the nearest rat source, but no interaction term (Fig. 4). In contrast, for islands in the eastern sector, three models were well supported by the data ($\Delta AIC_{c} < 1$, Table 3). We calculated the differences associated with the predicted values for each pair of models. The average difference between the predictions of pairs of models was very low $(1.73 \times 10^{-9} \pm 1.35)$ X 10⁻¹¹ (SD)). We concluded that the models were not biologically different and chose the simplest of the three models. The only parameter in the model selected for islands in the eastern sector was the log of distance to the nearest rat-infested island (Fig. 4).

In the western sector, the odds of rat presence increased by a factor of about 8.9 for each 10-fold increase in island area. In the eastern sector, the best model did not include an effect of island area. The effect of swim distance differed between eastern and western sectors. In the east, for every doubling of the distance to the nearest rat-infested island the odds of rat presence decreased by a factor of 0.36, whereas in the west, doubling the distance to the nearest rat source decreased the odds of rat occupancy by a factor of 0.09.

Model	AIC _c	ΔAIC_{c}	N-R ²
$logit(\pi) = 12.67 - 1.42*Log_2Dist + 0.80*West + 0.54*Log_{10}A - 0.34*(Log_2Dist - 10.25)X(Log_{10}A - 1.29)$	118.78	0	0.62
$logit (\pi) = 11.55 - 1.36^* Log_2 Dist + 0.78^* West + 0.83^* Log_{10} A$	119.48	0.7	0.61
logit (π) = 12.26 - 1.42* Log ₂ Dist + 0.60* West + 0.84* Log ₁₀ A - 0.24*(LogDist - 10.25)XWest	120.42	1.64	0.61
logit (π) = 11.53 - 1.36* Log ₂ Dist + 0.79* West + 0.82* Log ₁₀ A + 0.02* HumUse	121.61	2.83	0.61
logit (π) = 11.90 - 1.41* Log ₂ Dist + 0.84* West + 0.92* Log ₁₀ A - 0.38* (Log ₁₀ A - 1.29) X West	123.34	4.56	0.62

Table I. Models predicting the Probability of rat presence (π) .

Probability of rat presence (π) was best predicted by the logarithm of distance to the nearest rat-infested island (Log_2Dist), the nearest large landmass (East or West Falkland; *West*), and the logarithm of island area ($Log_{1d}A$).

Table 2. Models predicting the Probability of rat presence (π) for the west half of the archipelago.

Model	AIC	ΔAIC_{c}	N-R ²
$logit(\pi) = 27.49 - 2.91^* Log_2 Dist + 1.75^* Log_{10} A - 0.92^* (Log_2 Dist - 1.45) X(Log_{10} A - 10.75)$	32.84	0	0.84
logit (π) = 20.66 - 2.36* Log ₂ Dist + 2.19* Log ₁₀ A	33.91	1.07	0.82
logit (π) = 14.19 - 1.45* <i>Log</i> ₂ <i>Dist</i>	46.05	13.21	0.69
logit (π) = -0.34 - 0.02* $Log_{10}A$	93.49	60.65	0.0003

For the west half of the archipelago, the probability of rat occupancy decreased with the distance to the nearest rat-infested island ($Log_{J}Dist$) and increased with the logarithm of island area ($Log_{J}A$).

Table 3. Models predicting the Probability of rat presence (π) for the east half of the archipelago.

Model	AIC	ΔAIC_{c}	N-R ²
logit (π) = 8.72 - 1.02* <i>Log₂Dist</i>	82.93	0	0.44
logit (π) = 8.72 - 1.07* Log ₂ Dist + 0.42* Log ₁₀ A	83.34	0.41	0.46
$logit(\pi) = 10.11 - 1.18^* Log_2 Dist + 0.12^* Log_{10} A - 0.36^* (Log_2 Dist - 9.89) X(Log_{10} A - 1.78)$	83.76	0.83	0.48
logit (π) = -0.71 + 0.021* $Log_{10}A$	117.27	34.34	0.0001

In the east half of the archipelago, the probability of rat occupancy decreased with distance to the nearest rat-infested island (Log_2Dist). There was also substantial support for the model that predicted occupancy would increase with the logarithm of island area ($Log_{10}A$), however we chose the simpler of the two models.

Discussion

Our results indicate that the incidence of rats decreased with distance to the nearest ratinfested island. Also, for islands in the western sector of the archipelago, we found that the probability of rat occupancy increased with island area. In the eastern sector, we did not find a significant effect of island area on rat presence. Human activity did not appear to be a significant variable in the models, suggesting that it is not as important in determining the distribution of rats as distance from sources and island area. Here we consider the possible processes that might have produced these patterns. Specifically, we explore whether the observed patterns might be shaped by the balance between colonization and extinction as the classical metapopulation model suggests (Hanski et al. 1995), and argue that rats in the Falkland Islands satisfy some of the assumptions



Figure 4. Models for rat distribution included distance to the nearest rat source and island size. This figure presents the fraction of islands of a given size (bubble size is proportional to island size) predicted to have rats by our models as a function of distance to the nearest rat source. Colors of dots represent islands with (red) or without rats (blue). In both the west and east of the Falkland archipelago, the probability of rat presence on an island decreased with distance to the nearest rat-infested island. There was a higher probability of rat presence in the western sector than in the eastern sector and in the west rats were more likely to be found on larger than on smaller islands. In the east, there was no significant effect of island area on rat occupancy. Black dots (± SE) represent the fraction of islands with rats binned in groups of 500 m of swim distance.

of this model. To illustrate, we present preliminary evidence that rats migrate between islands in the Falklands, and that rat populations can go extinct. Then, we consider the implications of our data and models to management of rats in the Falklands.

Interpreting models

The models that we used to analyze the factors that determine the presence of rats in the Falkland Islands are descriptive. They document patterns, but by themselves, they do not reveal the processes that create them (Clinchy et al. 2002). Similar models are widely used in the study of metapopulations and can be used to estimate a variety of parameters, including extinction and colonization rates, from a snapshot of presence/ absence data (Driscoll 2007). Our data do not satisfy many of the assumptions needed to make these estimates. First, presence or absence of rats was assessed not as a snapshot, but over a period of several years (Falkland Islands Government 2013). Second, we only have data for a subset of islands and hence have to rely on distance to the nearest rat-infested island rather than on the distances to all possible island sources of rats for a focal island. Nevertheless, our data and results are consistent with the idea that rats in the Falklands represent a metapopulation.

As predicted by all classical metapopulation models (Hanski 2004), the occurrence of rats decreased with distance to potential rat sources. This result together with anecdotal observations suggests that rat subpopulations are linked by dispersal, but that exchanges of rats are more likely between adjacent rather than distant islands. Field observations support the conjecture that rats can move between subpopulations. For example, rats were successfully eradicated from Rookery Island in 2002 (and confirmed absent three years later using chew sticks), but eight years later we visited the island and found abundant fresh rat sign (Fig. 2). The most likely source of rats is Rat Island, 500 m away. Similar reinvasions have now been recorded on 8 islands between 2 and 6 years following successful eradication, over distances of up to 500 m (Falkland Islands Government 2012). It is more difficult to show that rat sub-populations go extinct, but 7 islands on which rats are currently known to be absent seemingly exhibit the legacy of being occupied by rats, with the absence of *T*. cobbi and low densities or absences of C. antarcticus, conditions which are otherwise only found on islands with rats present or shortly following rat eradication (Tabak et al. 2014a). It is possible that these islands had rats recently but that their local populations became extinct.

Although rats likely colonize islands and go locally extinct on islands, we doubt that the patterns of rat distribution revealed by our dataset are solely the steady state outcome of colonization and extinction. It is likely that these processes continue to occur, but it is also likely that the patterns that we have documented are the result of the interplay of environmental factors, both contemporary and historical. Nevertheless, human activity was not a significant variable in the models, suggesting that it is less important than distance to sources and island area. Russell and Clout (2004) also reported no correlation between an anthropogenic variable and Norway rat distribution in New Zealand. It appears that swimming is the most important mechanism by which rats move between islands in the Falklands.

How far can rats swim among islands?

The swimming abilities of rats are poorly understood but remarkably important, because they determine whether and when rats will reinvade islands that have been eradicated (Russell et al. 2010). The prevalence of rats decreased with distance from potential sources (Fig. 4), and very few islands further than 1 km away from a potential source of rats appeared to have been invaded. However, about 72% of the 54 islands within 500 m from the nearest source had rats, about 40% of 34 islands between 500 and 1,000 m away had rats on them, and of the 69 islands farther than 1,000 m from the nearest source, only two had rat populations (Table 4). Rats are also known to have swum at least 500 m to reinvade an island successfully cleared of rats (Falkland Islands Government 2013). This suggests that although there are limitations to how far rats can move among islands, these animals can swim relatively long distances, and consid-

Distance between islands (m)	Percent of islands occupied rats (%)
< 500	72
500–1,000	40
≥ 1,000	3

Table 4. Proportion of islands occupied by rats at different distances from the nearest source.

The probability of rat occupancy decreased with distance to the nearest rat source. Beyond 1,000 m, there was a low probability of rat occupancy.

erably farther that the 250 m initially suggested as a possible safe separation distance for eradication in the Falkland Islands (Brown 2001).

These results are surprising as the swimming endurance of rats decreases with water temperature and sea-surface temperatures in the Falkland Islands are cold (ranging from 2 °C in winter to 10° C in summer; Otley et al. 2008). At those temperatures, rats in the laboratory can only swim for less than 10 minutes (reviewed by Russell et al. 2008). Assuming a maximal speed of ≈ 25 m/min (Møller 1983), rats could potentially swim only between islands that are less than 250 m apart. Our data suggest that either Falklands rats are both hardier and better swimmers than laboratory rats or Falklands rats are frequently carried distances much larger than laboratory rats by oceanic currents. Rats in the Falklands appear capable of swimming relatively frequently (at least in ecological time) between islands separated by 500 m. Consequently, they might be able to swim even longer distances on occasion. Although the probability of a rat surviving a long distance swim and establishing a viable breeding population may be extremely low, the cumulative probability will increase over time. Factors that precipitate dispersal are unknown in the Falklands. One possible explanation is that rats swim to islands where whale strandings have recently occurred. These events provide an abundance of food for rats and occur with regular frequency in the Falklands (Otley 2012). Hypothetically, rats could smell these whale strandings from nearby islands and swim to this food source (Harper 2005). Another possible explanation is that large storms might facilitate rat dispersal (Losos et al. 1993).

Implications for management

Norway rats have reinvaded islands following eradications in the Falklands and in other archipelagoes. For example, three species of rats were eradicated from Perl Island, New Zealand in 2005 and Norway rats re-established a population across the island by 2007 (Russell et al. 2010). A relatively large proportion (29%) of islands from which Norway rats have been eradicated in New Zealand have been reinvaded (Clout and Russell 2006, Russell et al. 2008). Cost effective rat management strategies must account for the possibility that rats will reinvade after eradications, and must attempt to minimize this possibility. Although we cannot estimate with precision the rates of

rat colonization and dispersal among islands, nor the effect that distance and island area have on these, our data and results can still inform active rat eradication efforts in the Falklands.

Our models suggest that islands farther than 1,000 meters from the nearest ratinfested islands have a low probability (less than 0.05) of having rats, and hence of having been invaded. Indeed, of the 69 islands that are farther than 1,000 m from the nearest rat source in our dataset, only 2 have rat populations. We think that 1 km away from the nearest rat source is a reasonable threshold for eradication. This threshold does not guarantee that these islands will remain rat-free in perpetuity, but it represents a reasonable threshold that ensures a low probability of reinvasion after eradication (Russell et al. 2008).

Our data confirm the ability of rats to disperse among islands that are close to each other. If two or more islands are sufficiently close to each other as to have a high probability of reciprocal re-invasion, from a management perspective, these islands form a single "eradication unit," requiring simultaneous baiting (Robertson and Gemmel 2004). Eradication units can be informed by genetic profiling of different island populations (Abdelkrim et al. 2005). In a genetic profile of Falkland Islands rats, Tabak et al. (2014b) found that rats are capable of swimming distances of at least 830 m. We find the congruence between our current estimate of 1,000 m and the previous estimate of 830 m evidence of the robustness of these estimates. We argue that a threshold distance of 830–1,000 m is safe for eradication with a low probability that rats will recolonize. However, we recommend that prior to eradication attempts, rats on candidate islands and nearby rat-infested islands are sampled for genetic analyses to ensure that migration does not occur from rat sources to the candidate island.

Conclusion

Eradication of invasive rats can be an effective conservation tool, but the propensity of rats to return to islands following eradication can hamper the effectiveness of this strategy. We found, by modeling the distribution of Norway rats in the Falkland Islands, that rats are capable of moving, presumably by swimming, between islands. When we compared our estimate with the literature, we conclude that rats are unlikely to move distances of greater than 830-1,000 m between islands in the Falklands. We suggest the use of this distance for future eradication plans.

Acknowledgements

MT was funded by NSF Grant #0841298. We would like to thank Nick Rendell for permission to use data from the Falkland Islands Biodiversity Database. The comments of Jake Goheen and one anonymous reviewer benefitted previous versions of this manuscript.

References

- Abdelkrim J, Pascal M, Calmet C, Samadi S (2005) Importance of assessing population genetic structure before eradication of invasive species: examples from insular Norway rat populations. Conservation Biology 19(5): 1509–1518. doi: 10.1111/j.1523-1739.2005.00206.x
- Agnew DJ, Hill S, Beddington JR (2000) Predicting the recruitment strength of an annual squid stock: *Loligo gahi* around the Falkland Islands. Canadian Journal of Fisheries and Aquatic Sciences 57: 2479–2497. doi: 10.1139/f00-240
- Anderson DR (2008) Model Based Inferences in the Life Sciences: a Primer on Evidence. Springer, New York, 184 pp. doi: 10.1007/978-0-387-74075-1
- Armstrong PH (1994) Human impact on the Falkland Islands environment. The Environmentalist 14(3): 215–231. doi: 10.1007/BF01907141
- Atkinson IAE (1985) The Spread of Commensal Species *Rattus* to Oceanic Islands and their Effects on Island Avifaunas. In: Moors PJ (Ed.) Conservation of Island Birds, vol 3. ICBP Technical Publication, Cambridge, 35–81.
- Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer, New York, 488 pp. doi: 10.1126/science.1101617
- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305: 1955–1958.
- Bokhorst S, Huiskes A, Conevey P, Aerts R (2007) Climate change effects on organic matter decomposition rates in ecosystems from the Maritime Antarctic and Falkland Islands. Global Change Biology 13: 2642–2653. doi: 10.1111/j.1365-2486.2007.01468.x
- Brown D (2001) Guidelines for eradication of rats from islands within the Falklands group. A report to Falklands Conservation Falklands Conservation, Stanley, Falkland Islands.
- Clinchy M, Haydon DT, Smith AT (2002) Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics. The American Naturalist 159(4): 351–362. doi: 10.1086/338990
- Clout MN, Russell JC (2006) The eradication of mammals from New Zealand islands. In: Koike F, Clout MN, Kawamichi M, De Poorter M, Iwatsuki K (Eds) Assessment and Control of Biological Invasion Risks. IUCN, Gland, 127–141.
- Cree A, Daugherty CH, Hay JM (1985) Reproduction of a rare New Zealand repltile, the tuatara *Sphenodon punctatus*, on rat-free and rat-inhabited islands. Conservation Biology 9(2): 373–383. doi: 10.1046/j.1523-1739.1995.9020373.x
- Dagg AI, Windsor DE (1972) Swimming in northern terrestrial mammals. Canadian Journal of Zoology 50: 117–130. doi: 10.1139/z72-019
- Driscoll DA (2007) How to find a metapopulation. Canadian Journal of Zoology 85: 1031–1048. doi: 10.1139/Z07-096
- Falkland Islands Government (2012) The Falkland Islands Census 2012.
- Falkland Islands Government (2013) The Falkland Islands Biodiversity Database 2013.
- Fewster RM, Miller SD, Ritchie J (2011) DNA profiling a management tool for rat eradication. In: Fewster RM, Miller SD Ritchie J (Eds) Island Invasives: eradication and management. IUCN, Gland, 426–431.

- Fronhoffer EA, Kubisch A, Hilker FM, Hovestat T, Poethke HJ (2012) Why are metapopulations so rare? Ecology 93(8): 1967–1978. doi: 10.1890/11-1814.1
- Hall JR, Woods RW, Brooke MdL, Hilton GM (2002) Factors affecting the distribution of landbirds on the Falkland Islands. Bird Conservation International 12: 151–167.
- Hanski I (2004) Metapopulation theory, its use and misuse. Basic and Applied Ecology 5: 225–229. doi: 10.1016/j.baae.2004.03.002
- Hanski I, Moilanen A, Pakkala T, Kuussaari M (1996) The Quantitative Incidence Function Model and Persistence of an Endangered Butterfly Metapopulation. Conservation Biology 10(2): 578–590. doi: 10.1046/j.1523-1739.1996.10020578.x
- Hanski I, Pakkala T, Kuussaari M, Lei G (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72: 21–28. doi: 10.2307/3546033
- Harper GA (2002) Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.) population eruptions on Stewart Island/Rakiura. New Zealand Journal of Zoology 32: 155–162. doi: 10.1080/03014223.2005.9518408
- Hilton GM, Cuthbert RJ (2010) The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories. Ibis 152: 443–458. doi: 10.1111/j.1474-919X.2010.01031.x
- IUCN (2012) IUCN Red List of Threatened Species. Version 2012.1. http://www.iucnredlist.org
- Jones HP (2010) Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an island archipelago. Ecological Applications 20(5): 1204–1216.
- King WB (1985) Island Birds: Will the Future Repeat the Past? In: Moors PJ (Ed.) Conservation of Island Birds, vol 3. ICBP Technical Publication, Cambridge, 35–81. doi: 10.1890/09-1172.1
- Kurle CM, Croll DA, Tershy B (2008) Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences 105(10): 3800–3804. doi: 10.1073/pnas.0800570105
- Le Blanc JA (1958) Effect of chlorpromazine on swimming time of rats at different temperatures. Proceedings of the Scociety for Experimental Biology and Medicine 98: 648–650. doi: 10.3181/00379727-98-24138
- Levins RA (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society 15: 237–240.
- Levins RA (1970) Extinction. In: Gerstenhaber M (Ed.) Some Mathematical Questions in Biology. The American Mathematical Society, Providence, 75–107.
- Losos JB, Marks JC, Schoener TW (1993) Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia 95(4): 525–532.
- MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, 224 pp.
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83(8): 2248–2255. doi: 10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2
- McAdam JH (1980) Uncontrolled grazing and vegetation removal in the Falkland Islands. Environmental Conservation 7(3): 201–202. doi: 10.1017/S0376892900007578

- Moore DF (1986) Asymptotic properties of moment estimators for overdispersed counts and proportions. Biometrika 73(3): 583–588. doi: 10.1093/biomet/73.3.583
- Morley CG, Winder L (2013) The effect of the small Indian mongoose (*Urva auropunctatus*), island quality and habitat on the distribution of native and endemic birds on small islands within Fiji. Plos One 8(1): e53842. doi: 10.1371/journal.pone.0053842
- Nagelkerke NJD (1991) A note on a general definition of the coefficient of determination. Biometrika 78(3): 691–692. doi: 10.1093/biomet/78.3.691
- Otley H (2012) The composition of the cetacean community in the Falkland (Malvinas) Islands, southwest South Atlantic Ocean. Revista de Biología Marina y Oceanografía 47(3): 537–551. doi: 10.4067/S0718-19572012000300015
- Palomares MLD, Mohammed E, Pauly D (2006) On European expeditions as a source of historic abundance data on marine organisms: a case study of the Falkland Islands. Environmental History 11: 835–847. doi: 10.1093/envhis/11.4.835
- Pina DM, Cifuentes GG (2004) Las Aves de Chile: Nueva guia de campo. Ediciones del Naturalista, Santiago de Chile, 620 pp.
- Poncet S, Poncet L, Poncet D, Christie D, Dockrill C, Brown D (2011) Introduced mammal eradications in the Falkland Islands and South Georgia – Management. IUCN, Gland, 426–431.
- Robertson BC, Gemmel NJ (2004) Defining eradication units to control invasive pests. Journal of Applied Ecology 41(6): 1042–1048. doi: 10.1111/j.0021-8901.2004.00984.x
- Russell JC, Clout MN (2004) Modelling the distribution and interaction of introduced rodents on New Zealand offshore islands. Global Ecology and Biogeography 13: 497–507. doi: 10.1111/j.1466-822X.2004.00124.x
- Russell JC, Miller SD, Harper GA, MacInnes HE, Wylie MJ, Fewster RM (2010) Survivors or reinvaders? Using genetic assignment to identify invasive pests following eradication. Biological Invasions 12: 1747–1757. doi: 10.1007/s10530-009-9586-1
- Russell JC, Towns DR, Clout MN (2008) Review of rat invasion biology: Implications for island biosecurity. Science for Conservation 286: 1–54.
- Southby-Tailyour E (1985) Falkland Island Shores. Bloomsbury Publishing, London, 300pp.
- Strange IJ (1992) A field guide to the wildlife of the Falkland Islands and South Georgia. HarperCollins, London, 192 pp.
- Tabak MA, Poncet S, Passfield K, Martinez del Rio C (2014) Invasive species and land bird diversity on remote South Atlantic Islands. Biological Invasions 16(2): 341–352. doi: 10.1007/s10530-013-0524-x
- Tabak MA, Poncet S, Passfield K, Goheen JR, Martinez del Rio C (2014a) Rat eradication and the resistance and resilience of passerine bird assemblages in the Falkland Islands. Journal of Animal Ecology. doi: 10.1111/1365-2656.12312
- Tabak MA, Poncet S, Passfield K, Carling MD, Martinez del Rio C (2014b) The relationship between distance and genetic similarity among invasive rat populations in the Falkland Islands. Conservation Genetics 16(1): 125–135. doi: 10.1007/s10592-014-0646-4
- Towns DR, Atkinson IAE, Daugherty CH (2006) Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8: 863–891. doi: 10.1007/s10530-005-0421-z

- Waluda CM, Trathan PN, Rodhouse PG (1999) Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Marine Ecology Progress Series 183: 159–167. doi: 10.3354/meps183159
- Wiles GJ, Bart J, Beck REJ, Aguon CF (2003) Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. Conservation Biology 17(5): 1350–1360. doi: 10.1046/j.1523-1739.2003.01526.x
- Woods RW, Woods A (2006) Birds and Mammals of the Falkland Islands. WildGuides, Hampshire, 144 pp.



A subcontinental view of forest plant invasions

Christopher M. Oswalt¹, Songlin Fei², Qinfeng Guo³, Basil V. Iannone III², Sonja N. Oswalt¹, Bryan C. Pijanowski², Kevin M. Potter⁴

I US Forest Service, Southern Research Station. Forest Inventory and Analysis. 4700 Old Kingston Pike, Knoxville, TN 37922, USA 2 Purdue University, Department of Forestry and Natural Resources, 715 W. State Street, West Lafayette, IN 47907, USA 3 US Forest Service, Southern Research Station, Eastern Forests Environmental Threat Assessment Center. 200 W.T. Weaver Blvd. Asheville, NC 28804, USA 4 North Carolina State University, Department of Forestry and Environmental Resources. 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA

Corresponding authors: Christopher M. Oswalt (coswalt@fs.fed.us); Songlin Fe (sfei@purdue.edu)

Academic editor: Uwe Starfinger | Received 1 August 2014 | Accepted 19 November 2014 | Published 16 January 2015

Citation: Oswalt CM, Fei S, Guo Q, Iannone III BV, Oswalt SN, Pijanowski BC, Potter KM (2015) A subcontinental view of forest plant invasions. NeoBiota 24: 49–54. doi: 10.3897/neobiota.24.8378

Abstract

Over the last few decades, considerable attention has focused on small-scale studies of invasive plants and invaded systems. Unfortunately, small scale studies rarely provide comprehensive insight into the complexities of biological invasions at macroscales. Systematic and repeated monitoring of biological invasions at broad scales are rare. In this report, we highlight a unique invasive plant database from the national Forest Inventory and Analysis (FIA) program of the United States Forest Service. We demonstrate the importance and capability of this subcontinental-wide database by showcasing several critical macroscale invasion patterns that have emerged from its initial analysis: (1) large portion of the forests systems (39%) in the United States are impacted by invasive plants, (2) forests in the eastern United States harbor more invasive species than the western regions, (3) human land-use legacies at regional to national scales may drive large-scale invasion patterns. This accumulated dataset, which continues to grow in temporal richness with repeated measurements, will allow the understanding of invasion patterns and processes at multi-spatial and temporal scales. Such insights are not possible from smaller-scale studies, illustrating the benefit that can be gained by investing in the development of regional to continental-wide invasion monitoring programs elsewhere.

Keywords

Invasive plants, forest ecosystems, macroscale, spatiotemporal patterns

Introduction

Exotic invasions can significantly alter the structure, function, and services of ecosystems (Vitousek et al. 1997, Simberloff et al. 2012, Fei et al. 2014). Over the last few decades, considerable attention has focused on small-scale studies of invasive plants and invaded systems. Unfortunately, small scale studies rarely provide comprehensive insight into the complexities of biological invasions at macroscales or across scales (Pauchard and Shea 2006). There is a need for regional to continental-scale invasion data and complementary analyses to facilitate our understanding of scale-dependent phenomena and cross-scale interactions (Soranno and Schimel 2014). Additionally, debate over the detectability of biotic interactions across broad scales (Araújo and Rozenfeld 2014) can only be comprehensively approached through datasets that cross multiple geographic scales. This understanding needs to be incorporated into management plans to ensure the sustainability of vital ecosystem services such as those that are provided by forest ecosystems.

Monitoring plants and animals at a national scale can be difficult and expensive, so databases of this kind are rare. The national Forest Inventory and Analysis (FIA) program in the United States (U.S.) has been monitoring invasive plants (here defined as alien plants whose introduction does or is likely to cause economic or environmental harm or harm to human – see U.S. Executive Order 13112 (1999)) occurrence and spread across all public and private U.S. forests for more than a decade, but to date no attempts have been made to aggregate and analyze data at a national scale. The consistent nature of the FIA sample design (Bechtold and Patterson 2005), and its national sampling intensity of approximately one plot per approximately 2,400 forested hectares (ca. 120,000 total plots), provides a unique view of plant invasions across space and time. The design for FIA inventory plots consists of four 7.3 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold and Patterson 2005) that are measured once every 5–7 years in the eastern U.S. and once every 10 years in the western U.S.

The objective of this short communication is to showcase the importance and capability of this unique invasive plant database to encourage its utilization by research and management communities, and to promote the establishment of such large-scale monitoring programs in other regions and continents. To meet these objectives, we present summary results both across the nation and within individual regions to illustrate how such a program can produce new insights into invasion ecology and the potential drivers of invasions that are not possible from smallerscale investigations.

Due to the considerable number of invasive plants in the U.S., data are collected based on region-specific monitoring lists of problematic forest plant invaders agreed upon by invasive plant experts (Oswalt et al 2012). We extracted invasive plant data from the FIA program and calculated summary statistics for each region, as well as across the entire nation. As invasive plants of concern differ by region and, in some cases, by state, we normalized the data to be able to characterize nation-wide patterns using an invasion-intensity metric. Normalization was achieved by calculating



Figure 1. Forest plant invasion intensity (percent of forested plots with an invasive plant recorded for a given county based on FIA sampling) for the United States including estimates of region-wide invasion intensity.

the number of forested subplots with at least one invasive species present in a given county divided by the total number of forested subplots monitored in the same county. Therefore, we define invasion-intensity as the percent of forested subplots within a county containing any invasive plants that are on the region/state-specific monitoring lists. We then mapped the subcontinental spatial distribution of invasive plants based on this invasion-intensity metric. In addition, we mapped the expansion of *Imperata cylindrilca* to showcase the capability of the database in studying the temporal dynamic of invasive plants.

We observed multiple macroscale invasion patterns based on our simple initial analyses that would not have been detectable from smaller scale studies, highlighting the utility of national-level sampling efforts. First, 39% of forested plots sampled nationwide for invasive plants contained at least one invasive species, revealing that a significant portion of the more than 300 million hectares of U.S. forests have been invaded. Clearly, the footprint of invasives is significant at large scales. Hawaii had the highest invasion-intensity (70%). Second, forests in the eastern U.S. had higher invasion-intensity (46%) than in the west (11%), while forests in Alaska (6%) and the Intermountain region (6%) had the lowest invasion intensity (Figure 1). Third,

Rank	South	North	Intermountain West	Pacific	
1	Lonicera japonica	Rosa multiflora	Bromus tectorum	Bromus tectorum	
2	Ligustrum sinense/vulgare	Phalaris arundinacea	Cirsium arvense	Rubus armeniacus	
3	Rosa spp.	Alliaria petiolata	Centaurea biebersteinii	Hypericum perforatum	
4	Lespedeza cuneata	Lonicera japonica	Cynoglossum officinale	Cirisium arvense	
5	Microstegium vimineum	Rhamnus cathartica	Carduus nutans	Taeniatherum caput-medusae	

Table 1. Top five most inventoried forest invasive plants by the FIA program within each region of the United States.

clusters of more highly invaded counties may suggest a strong relationship between invasion intensity and human land-use legacies at regional to national scales. Specifically, highly fragmented landscapes (as in the North Central region) and major travel corridors (as in the Piedmont of the Southeast) tended to exhibit higher invasionintensity (Figure 1). In addition, we observed variability in invasion patterns across both climate regimes and elevation gradients suggesting further investigations into how climate change could facilitate or impede future invasions are needed.

The dataset also revealed it will be important to understand what factors have driven the expansion of the most prevalent invaders in forest ecosystems, such as *Rosa multiflora* in the north, *Lonicera japonica* in the south, and *Bromus tectorum* in the Intermountain and Pacific regions (Table 1). The same is true for invaders that are currently quickly expanding, such as the expansion of *Imperata cylindrica* from an epicenter located near Mobile Bay (Figure 2) in the southern U.S. At fine scales, repeatedly measured FIA plots will allow for investigating the drivers of such expansions. The accumulated dataset, which continues to grow in temporal richness, with its inclusion of multiple measurements of the same plots will allow researchers to reveal temporal invasion patterns and processes at large spatial scales.

As other large-scale datasets (e.g., climate, elevation, land cover, soils, human population and natural resource management practices, etc.) become more readily available, we can conduct more comprehensive investigations into ecologically and economically important questions such as: What are the underlying processes that produce the macroscale invasion patterns and how do these processes differ and/or interact across scales? What are the traits of both invaders and invaded ecosystems that facilitate invasion? And what are the cross-scale interactions that lead to the emergence of macroscale patterns such as those observed in this report? Integration of these data and other invasive taxonomic groups, such as insects, birds, and mammals, could provide macrosystems ecologists with broader "systems" perspective of invasive ecology.

While these data aid the development of a more comprehensive understanding of plant invasions within forests of the United States, there were challenges to assembling them in their current form and obstacles to their analytical use. To harmonize the data, several normalizations had to be performed and some comparability across regional boundaries at finer scales was lost. Nonetheless, no comparable dataset exists, and the macroscale invasion patterns that have emerged from even the relatively simple analysis of this dataset clearly reveals the benefit of large-scale invasion monitoring program.



Figure 2. Spatial progression of *Imperata cylindrica* based on multiple measurements of forested plots from the FIA sampling grid. Time 1 represents data collected from 2001 to 2005 and Time 2 from 2006 to 2011.

Acknowledgements

The data presented here were collected by numerous hard-working individuals throughout the United States, and we thank them for their tireless efforts to document the presence of invasive plants on our nation's forests. Additionally, we are grateful to Keith Moser, Cassandra Kurtz, Beth Schulz, Christopher Witt, and Andrew Gray for assembling the data from their respective regions. This research was partially supported by the National Science Foundation (grant # 1241932).

References

- Araújo MB, Rozenfeld A (2014) The geographic scaling of biotic interactions. Ecography 37: 406–415.
- Bechtold WA, Patterson PL (2005) The enhanced forest inventory and analysis program: national sampling design and estimation procedures. US Department of Agriculture Forest Service, Southern Research Station.

- Fei S, Phillips J, Shouse M (2014) Biogeomorphic impacts of invasive species. Annual Reviews of Ecology, Evolution, and Systematics 45: 69–87. doi: 10.1146/annurev-ecolsys-120213-091928
- Oswalt C, Oswalt S, Zimmerman L (2012) Updating the southern nonnative plant watch list: the future of NNIP Monitoring in the south. In: Morin R, Liknes G (Eds) Moving from status to trends: Forest Inventory and Analysis (FIA) symposium 2012; 2012 December 4–6; Baltimore, MD. Gen. Tech. Rep. NRS-P-105. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, 274–277. [CD-ROM]
- Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399–413. doi: 10.1007/s10530-005-6419-8
- Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vila M (2012) Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28: 58–66. doi: 10.1016/j.tree.2012.07.013
- Soranno PA, Schimel DS (2014) Macrosystems ecology: big data, big ecology. Frontiers in Ecology and the Environment 12: 3–3. doi: 10.1890/1540-9295-12.1.3
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7:737–750.

SHORT COMMUNICATION



Aliens in Transylvania: risk maps of invasive alien plant species in Central Romania

Heike Zimmermann¹, Jacqueline Loos¹, Henrik von Wehrden^{1,2,3}, Joern Fischer¹

Institute of Ecology, Faculty of Sustainability, Leuphana University Lüneburg, Scharnhorststr. 1, 21335 Lüneburg, Germany 2 Centre for Methods, Leuphana University Lüneburg, Scharnhorststr. 1, 21335 Lüneburg, Germany 3 Research Institute of Wildlife Ecology, Savoyen Strasse 1, Vienna 1160, Austria

Corresponding author: Heike Zimmermann (heike.zimmermann@uni-leuphana.de)

Academic editor: Ingolf Kühn | Received 24 April 2014 | Accepted 15 September 2014 | Published 16 January 2015

Citation: Zimmermann H, Loos J, von Wehrden H, Fischer J (2015) Aliens in Transylvania: risk maps of invasive alien plant species in Central Romania. NeoBiota 24: 55–65. doi: 10.3897/neobiota.24.7772

Abstract

Using the MAXENT algorithm, we developed risk maps for eight invasive plant species in southern Transylvania, Romania, a region undergoing drastic land-use changes. Our findings show that invasion risk increased with landscape heterogeneity. Roads and agricultural areas were most prone to invasion, whereas forests were least at risk.

Keywords

Erigeron annuus, MAXENT, Robinia pseudoacacia, Romania, Solidago canadensis, Xanthium strumarium

Introduction

Species distribution models are a useful tool in biological invasion risk management (Jiménez-Valverde et al. 2011). They allow a rapid assessment of the distribution of alien species, which may serve to identify areas of high invasibility and to understand the mechanisms behind the establishment and spread of alien species (Zimmermann et al. 2011).

We focused our study on southern Transylvania, in Central Romania, where temporary or permanent abandonment of agricultural land is common. Knowledge on the introduction history of invasive plant species and their current distribution in this region is largely missing, although several common alien plant species are among the world's 100 worst invaders (DAISIE 2013; GISD 2013). To address this knowledge gap, we aimed to identify predictors of the distribution of eight highly invasive species.

Methods

Study area

Our study area comprised an area of 7,440 km² (Fig. 1). It is a heterogeneous, hilly, rural landscape, at elevations from 230 to 1100 m, and characterized by a mosaic of different land cover types supporting high farmland biodiversity (Loos et al. 2014). Small-scale semi-subsistence farming with little use of machinery or agrochemicals, as well as extensively used hay meadows and grasslands are typical for the region. The small-scale mosaic pattern of different land cover types prevails throughout the study area, although the North-West has a relatively higher percentage of arable land, the South has a relatively higher percentage of pastures, and the central part a higher percentage of forests (Hanspach et al. 2014). Like many other parts of Eastern Europe, Romania has experienced drastic socio-economic changes, with the collapse of the



Figure 1. Location of our study area in Romania. Inside the enlarged map of our study area the cities Mediaş and Sighişoara are outlined and black points represent the presence points of all eight study species.



Figure 2. Population census data from 1990, 2000 and 2005 for a subsample of 22 communes across the study area. One commune typically includes four villages. In Romania the communist regime and its collapse in 1989 triggered mass emigration from these areas.

communist regime in 1989, and its accession to the European Union in 2007 (Kuemmerle et al. 2009). Among other changes, the communist regime and its collapse triggered mass emigration from some areas, resulting in widespread farmland abandonment (Fig. 2).

Sampling

In summer 2013, we mapped presences of eight prominent alien plant species across the study area using a handheld global positioning system (Table 1, see also Suppl. material 1). Our sampling covered a large variety of landscape elements within 50 km of the town of Sighişoara (Fig. 1). In each local valley, we undertook at least two extended survey walks that lasted between 30 and 180 minutes. We sampled along roads, but also tracked species off-road, by walking towards the top of the hills bordering a given valley (see Suppl. material 2 for details). Furthermore, we took sample points whenever we observed an invasive species during our other field activities. For *Robinia pseudoacacia* we did not record planted trees, but only naturally dispersed individuals. We did not measure the distance to the next adult tree, but the minimum distance was approx. 100 m and for most recordings adult trees were not in sight. We also included vegetation sampling data from 2012, which was based on a randomized stratified design. The minimum distance between sampling points was 30 m. In combination, our sampling approach covered a wide range of environments across the study area.

Species	Family	Common name	Life strategy	Origin	Reproduction/dispersal	Presence points
Amaranthus retroflexus L.	Amaranthaceae	Redroot amaranth	annual herb ~1 m	N Am	monoecious, wind pollinated, dispersed by wind, water and animals	45
Asclepias syriaca L.	Apocynaceae	Common milkweed	perennial herb ~1–2 m	N Am	insect pollinated, seeds wind dispersed, and vegetative reproduction (rhizomes)	65
<i>Conyza</i> <i>canadensis</i> (L.) Cronquist	Asteraceae	Canadian horseweed	annual herb ~1 m	N Am	insect pollinated, self- and cross- fertilization, seeds wind dispersed	35
<i>Erigeron annuus</i> (L.) Pers.	Asteraceae	Annual fleabane	annual herb ~1 m	N Am	insect pollinated, self- and cross- fertilization, winged achenes dispersed by wind and animals	475
<i>Fallopia japonica</i> (Houtt.) Ronse Decr.	Polygonaceae	Japanese knotweed	perennial herb ~3 m	Asia	insect pollinated, dioecious, winged achenes dispersed by wind, water, animals, and reproduces vigorously by rhizomes	69
Robinia pseudoacacia L.	Fabaceae	Black locust	deciduous tree ~30 m	N Am	insect pollinated, seeds wind dispersed, reproduces vigorously by root suckering and stump sprouting	264
Solidago canadensis L.	Asteraceae	Canadian goldenrod	perennial herb ~2.5 m	N Am	insect pollinated out-crossing, wind dispersed achene with pappus, and vegetative reproduction (rhizomes)	298
Xanthium strumarium L.	Asteraceae	Common cocklebur	annual herb ~1 m	N Am	wind-pollinated, monoecious, self- and cross- fertilization, apomixis, seeds dispersed by animals and water	236

Table 1. Overview of study species and number of sampling points (N Am = North America).

Analysis

We derived invasion risk maps for each species individually. To this end, we applied the Maximum Entropy algorithm (MAXENT), which is based on presence only data to map the likely current distribution for each species in our study area (Phillips et al. 2006; Elith et al. 2011; Merow et al. 2013). Our approach to model the likely current distribution based on presence only data is in line with our assumption that the expansion of our species has not yet reached equilibrium, making the use of observed absences misleading (Jiménez-Valverde et al. 2011). Clamping was activated as well as random seed, and we made an internal validation with 50 replicates and 20 % random test percentage. Predictors encompassed information on the topography, land use and potential distribution corridors (Table 2). Slope and terrain ruggedness (the variation in altitude) did not improve any of the models. Our final models therefore included four predictors (road and village distance, heterogeneity, and land cover classes). Each of these predictors was re-sampled to a cell size of 30 x 30 m within ArcGIS, which

Predictor	Description	Relative importance in the MAXENT model
Road distance	minimum distance to the closest road	18 to < 40 % (A. retroflexus, A. syriaca, C. canadensis) 45–48 % (E. annuus, R. pseudoacacia, S. canadensis) >50%–56% (F. japonica, X. strumarium) for all species h.s. high with decreasing distance
Village distance	minimum distance to the closest village	15 % (<i>S. canadensis</i>) high h.s. at 3-4 km for remaining species values <10%
Heterogeneity (CNES 2007, Distribution Spot Image SA)	variation in the panchromatic channel of SPOT 5 satellite imagery	>20 %-35% (A. syriaca, C. canadensis, E. annuus, F. japonica, S. canadensis, X. strumarium) >40%-46% (A. retroflexus, R. pseudoacacia) for all species h.s. high with increasing heterogeneity
Corine land cover classes (Corine 2006 Land Cover Map, EEA (2006) Corine land cover 2000 A seamless vector database (European Environment Agency, Copenhagen)	 (1) broad leaved forest (2) coniferous and mixed forest (3) water (4) inland marshes (5) natural areas (sparsely vegetated, bare rocks, natural grasslands) (6) transitional woodland-shrub habitats (7) artificial surfaces (8) agriculture (9) pasture (10) Land principally occupied by agriculture with significant areas of natural vegetation 	 15 % (X. strumarium high h.s. for class 8) 22% (A. retroflexus high h.s. for class 4) 23 % (A. syriaca high h.s. for classes 8, 9) 35% (C. canadensis high h.s. for classes 8, 10) for remaining species values <15 %

Table 2. Predictors for the MAXENT model. All predictors have a 30 x 30 m resolution. (h.s. = habitat suitability).

thus equals the resolution of our risk maps. To calculate the potential areas suitable for each species a threshold rule was applied to convert continuous suitability surfaces into binary outputs. We selected the threshold "maximum training sensitivity plus specificity logistic threshold", which focuses on the correct classification of presences and background points (Jiménez-Valverde and Lobo 2007).

For each grid cell, we then calculated the mean probability of occurrence over all eight species. This resulted in a map of general invasion risk for the study area, referred to "the invasibility map" hereafter.

Results

Single distribution models of the eight study species all had high discrimination performances with AUC values ranging from 0.8 to 0.9 (Elith 2002). Standard deviation of the output grids showed no signs of autocorrelation (see also Suppl. material 2). Road distance and heterogeneity were the most important predictors (Table 2). Corine land cover classes substantially improved the MAXENT model of three species, with agricultural areas, pastures and land principally occupied by agriculture with significant areas of natural vegetation, having the highest risk of invasion. Forest was at least risk of being



Figure 3. The likely current distribution for **a** *Erigeron annuus* and **b** *Asclepias syriaca* in our study area. **c** Shows the invasibility, calculated as the mean probability of occurrence over all eight study species.

invaded. With 31 % potential habitat, *Erigeron annuus* has the largest potential distribution and with 8 %, *Asclepias syriaca* had the lowest (Fig. 3 a, b). Risk maps of all species show a high invasibility of distribution corridors such as roads and rivers (see Suppl. material 3). The overall invasibility map therefore shows a network structure with the highest invasibility close to distribution corridors stretching across the whole study area (Fig. 3c). However, the invasibility was highest in heterogeneous areas, which is where it also reached furthest away from roads.

Discussion

Our risk maps show that the eight invaders considered have great potential to further expand their distributions. All except for one study species are wind dispersed, which is an effective long distance dispersal method (Cain et al. 2000). Roads serve as invasion corridors, enabling the species establishment inside disturbed road margins (Birdsall et al. 2011). Environments at greatest risk of invasion away from roads appeared to be heterogeneous agricultural areas. Landscape heterogeneity is beneficial for native species in farming landscapes, because it offers a greater variety of habitats (Fischer and Lindenmayer 2007). However, invasive species also appear to benefit from this variety. A positive correlation of native and invasive plant species richness in relation to landscape heterogeneity was also shown for the Rocky Mountain National Park in the USA (120-960 m radius scale; Kumar et al. 2006), for rural and urban areas in Germany (32 km² scale; Deutschewitz et al. 2003), as well as for rural areas and woodlands in Catalonia (100 km² scale; Bartomeus et al. 2012). Furthermore, heterogeneous landscapes offer more edge environments which are subject to higher levels of propagule pressure and disturbance, and therefore a higher abundance of invasive plant species (Vilà and Ibáñez 2011). Like many invasive species, our study species are adapted to disturbance through their short life cycles, rapid germination, persistent seed banks, or vegetative reproduction (Rejmánek and Richardson 1996; Kolar and Lodge 2001).

We observed that areas with a high heterogeneity often coincides with areas that experienced the most widespread emigration following the collapse of communism. Socio-economic effects at regional or local scales are rarely considered in invasion science (Vilà and Pujadas 2001, Guo et al. 2012). This is a potentially important oversight. For example, farmland abandonment and land-use change can facilitate high abundances of alien plant species (Hobbs 2000; Cramer et al. 2008). Decades of cultivation may deprive native seed banks and altered soil conditions may no longer be suitable for native species (Cramer et al. 2008). In comparison to native species, species new to this region may possess traits that make them better colonizers of abandoned fields. They benefit from increased human mediated propagule pressure (propagule bias), are often stronger competitors (enemy release, novel weapons), and once established may further transform their environment, making it even less suitable for native species – thereby creating self-perpetuating

alien monocultures (Catford et al. 2012). Our study area continues to undergo socio-economic changes. With our main project ("Fostering sustainable development in Eastern Europe" http://peisajesustenabile.wordpress.com/) we aim to provide leverage points for enabling sustainable land use practices. Based on the results of this study we recommend to preserve the remaining intact forests, which seem to be least in risk of invasions and to further investigate the role of land abandonment and land use change in our study area.

Acknowledgments

We thank all the people in the field who helped us to track down aliens in Transylvania. We are also thankful to P. Brandt and P. Fust for their technical advice. This study was funded by a Leuphana small research grant (HZ) and through a Sofja Kovalevskaja Award by the Alexander von Humboldt Foundation (JL, JF).

References

- Bartomeus I, Sol D, Pino J, Vicente P, Font X (2012) Deconstructing the native–exotic richness relationship in plants. Global Ecology and Biogeography 21: 524–533. doi: 10.1111/j.1466-8238.2011.00708.x
- Birdsall JL, McCaughey W, Runyon JB (2011) Roads impact the distribution of noxious weeds more than restoration treatments in a lodgepole pine forest in Montana, USA. Restoration Ecology 20: 517–523. doi: 10.1111/j.1526-100X.2011.00781.x
- Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217–1227. doi: 10.2307/2656714
- Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA, Rejmánek M, Bellingham PJ, Pergl J, Horvitz CC, Hulme PE (2012) The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. Perspectives in Plant Ecology, Evolution and Systematics 14: 231–241. doi: 10.1016/j. ppees.2011.12.002
- Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology & Evolution 23: 104–112. doi: 10.1016/j. tree.2007.10.005
- DAISIE (2013) Delivering Alien Invasive Species Inventories for Europe. http://www.europealiens.org/default.do [Accessed 10 October 2013]
- Deutschewitz K, Lausch A, Kühn I, Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Global Ecology and Biogeography 12: 299–311. doi: 10.1046/j.1466-822X.2003.00025.x
- Elith J (2002) Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In: Ferson S, Burgman M (Eds) Quantitative methods for conservation biology. Springer, New York, 39–58.

- Elith J, Phillips SJ, Hastie T, Dudik M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17: 43–57. doi: 10.1111/j.1472-4642.2010.00725.x
- Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16: 265–280. doi: 10.1111/j.1466-8238.2007.00287.x
- GISD (2013) Global Invasive Species Database. http://www.issg.org/database/welcome/ [Accessed 10 Oktober 2013]
- Guo Q, Rejmanek M, Wen J (2012) Geographical, socioeconomic, and ecological determinants of exotic plant naturalization in the United States: insights and updates from improved data. NeoBiota 12: 41–55. doi: 10.3897/neobiota.12.2419
- Hanspach J, Hartel T, Milcu A, Mikulcak F, Dorresteijn I, Loos J, von Wehrden H, Kuemmerle T, Abson DJ, Kovács-Hostyánszki A, Báldi A, Fischer J (2014) A holistic approach to studying social-ecological systems and its application to Southern Transylvania. Ecology and Society 19(4): 32. doi: 10.5751/ES-06915-190432
- Hobbs RJ (2000) Land-use changes and invasions. In: Mooney HA, Hobbs RJ (Eds) Invasive Species in a Changing World. Island Press, Washington DC, 55–64.
- Jiménez-Valverde A, Lobo JM (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecologia 31: 361–369. doi: 10.1016/j. actao.2007.02.001
- Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragon P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biological Invasions 13: 2785–2797. 10.1007/s10530-011-9963-4
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16: 199-204. doi: 10.1016/S0169-5347(01)02101-2
- Kuemmerle T, Müller D, Griffiths P, Rusu M (2009) Land use change in Southern Romania after the collapse of socialism. Regional Environmental Change 9: 1–12. doi: 10.1007/ s10113-008-0050-z
- Kumar S, Stohlgren TJ, Chong GW (2006) Spatial heterogeneity influences native and nonnative plant species richness. Ecology 87: 3186–3199. doi: 10.1890/0012-9658(2006)87
- Loos J, Dorresteijn I, Hanspach J, Fust P, Rakosy L, Fischer J (2014) Low-intensity agricultural landscapes in Transylvania support high butterfly diversity: implications for conservation. PloS One 9: e103256. doi: 10.1371/journal.pone.0103256
- Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36: 1058–1069. doi: 10.1111/j.1600-0587.2013.07872.x
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. doi: 10.1016/j.ecolmodel.2005.03.026
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655–1661. doi: 10.2307/2265768
- Vilà M, Ibáñez I (2011) Plant invasions in the landscape. Landscape Ecology 26: 461–472. doi: 10.1007/s10980-011-9585-3

- Vilà M, Pujadas J (2001) Land-use and socio-economic correlates of plant invasions in European and North African countries. Biological Conservation 100: 397–401. doi: 10.1016/ S0006-3207(01)00047-7
- Zimmermann H, von Wehrden H, Damascos MA, Bran D, Welk E, Renison D, Hensen I (2011) Habitat invasion risk assessment based on Landsat 5 data, exemplified by the shrub *Rosa rubiginosa* in southern Argentina. Austral Ecology 36: 870–880. doi: 10.1111/j.1442-9993.2010.02230.x

Supplementary material I

Table of species localities.

Authors: Heike Zimmermann, Jacqueline Loos, Henrik von Wehrden, Joern Fischer Data type: (measurement/occurence/multimedia/etc.)

- Explanation note: Table of all species localities (latitude and longitude in decimal degrees, WGS 84).
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Supplementary material 2

Check for sampling bias.

Authors: Heike Zimmermann, Jacqueline Loos, Henrik von Wehrden, Joern Fischer Data type: (measurement/occurence/multimedia/etc.)

- Explanation note: We checked our dataset for sampling bias, that is the distribution of presence points (N = 1484) at different road distances.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Supplementary material 3

Risk maps for all eight study species.

Authors: Heike Zimmermann, Jacqueline Loos, Henrik von Wehrden, Joern Fischer Data type: (measurement/occurence/multimedia/etc.)

Explanation note: Risk maps for all eight study species derived from the MAXENT model. Copyright notice: This dataset is made available under the Open Database License

(http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.