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Why are there so many exotic Springtails in Australia? A review.

Penelope Greenslade[1, 2]

[1] Environmental Management, School of School of Health and Life Sciences, Federation University, Ballarat, Victoria 3353, Australia

[2] Department of Biology, Australian National University, GPO Box, Australian Capital Territory 0200, Australia

E-mail: p.greenslade@federation.edu.au

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Abstract

Native invertebrate assemblages in Australia are adversely impacted by invasive exotic plants because they are replaced by exotic, invasive invertebrates. The reasons have remained obscure. The different physical, chemical and biotic characteristics of the novel habitat seem to present hostile conditions for native species. This results in empty niches. It seems the different ecologies of exotic invertebrate species may be better adapted to colonise these novel empty niches than native invertebrates. Native faunas of other southern continents that possess a highly endemic fauna, such as South America, South Africa and New Zealand, may have suffered the same impacts from exotic species but insufficient survey data and unreliable and old taxonomy makes this uncertain. Here I attempt to discover what particular characteristics of these novel habitats are hostile to native invertebrates.

I chose the Collembola as a target taxon. They are a suitable group because the Australian collembolan fauna consists of a high percentage of endemic taxa, but also exotic, non-native, species. Most exotic Collembola species in Australia appear to have originated from Europe, where they occur at low densities (Fjellberg 1997, 2007). Once in Australia many become invasive forming large populations. This occurs most frequently in exotic grasses and other weeds, but also even in native vegetation. I provide here species records from a number of sites that have been both invaded and colonised by exotic Collembola as well as those that still only carry native species, and document the differences between sites and faunas as far as is known. I suggest that a major factor is likely a change in microflora because of higher nutrient levels on invaded sites, particularly nitrogen and phosphorus from either fertilisers or rapid decomposition rates of exotic plants. The traits of exotic species, where known, tend to be *r* selected and so have a competitive advantage over the mainly K or A selected native species is another factor.

Keywords invasion biology | decomposition | soil nutrients | exotic plants | competitive traits

1. Introduction

The threats exotic (= non-native) invertebrate species pose to native faunas have been highlighted in recent publications, showing that they frequently outcompete native species and even cause extinctions (Gurevitch & Padilla 2004 and included references). McGeoch et al (2015) list ten ways in which invasive insects can impact on native insects. They are by competition, predation, hybridisation, transmission of disease, parasitism, poisoning, biofouling, herbivory, chemical, physical or structural impact or by causing impacts by interacting with other alien species. More specifically, the invasion and establishment of an exotic species into an ecosystem has the potential to modify interactions between species at all trophic levels. This phenomenon is described as a trophic cascade (French & Major 2001, Le Maitre et al. 2011, Marchante et al. 2015, Walsh et al. 2016). In addition, exotic species present economic threats by loss of crops, and the magnitude of their effects varies

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not only with climatic factors but also with soil nutrient availability as they can monopolise resources and, with different physiologies, can alter mineral composition of soils (Tabassum & Leishman 2016). The cost in lost ecosystem services that invasive species can pose in native environments has been estimated, in one fresh water environment, to be in the millions of dollars (Walsh et al. 2016).

Exotic invertebrates are a particular threat in Australia because of the high endemism of the native fauna, in particular, to short-range endemic species by outcompeting them. Intuitively, native species should be protected, not only because of the ecosystem services that they and their habitats provide, but also because these species are a store of information on the origins and evolution of Australian fauna and flora and their biogeographical relationships.

It is important therefore to investigate what habitat characteristics permit colonisation by exotic species so their impacts can be assessed, contained and even, where possible, eliminated.

I use as focus group a common soil arthropod taxon, the Collembola. This is because the Australian collembolan fauna is large and the total number of species is nearly 350 described native and endemics with a further 700 not yet described (Greenslade 2018). This number includes eighty-five proven and probable exotic Collembola species identified for Australia, increased from the number of 35 recorded by Greenslade & Ireson (1986) (Tab. 1). Of the total number of exotic species recorded from Australia, sixty species are confirmed, another 20 species are probables and five possibly misidentified (Tab. 1). The native collembolan fauna of Australia is highly endemic at species and generic level and is a proven measure of disturbance (Greenslade 1994, 1997, 2007).

Several publications within and outside Australia have shown that species compositions rather than taxa abundances are impacted by exotic plants (Greenslade et al. 2014; Coyle et al. 2017; Rusterholz et al. 2014). Much earlier work evaluating the deleterious effects of exotic collembolan species has identified fauna to higher levels but not to species (see Coyle et al. 2017), so obscuring their species-specific habitat preferences. This is particularly a problem in understanding processes following invasions of Collembola to Australia where there is a clear distinction between native species and non-native species in their habitats and ecologies. Specimens collected must therefore be identified to species and counted rather than only counts of genera, families or higher taxa. In Australia, identification of exotic species is straight forward as many have originated from the Northern Hemisphere where the fauna is well known (Greenslade & Convey 2012). Normally morphology is sufficient to identify species, but molecular sequence data can be practical if recorded already online (Porco et al. 2012, Cicconardi et al. 2017).

There exists a considerable body of relevant information on Collembola faunas from surveys carried out throughout Australia in many different types of ecosystems and vegetation types documented over fifty years. Firstly, I summarise this work by documenting existing data on the characteristics of habitats that are have been invaded by exotic species and those that are not. Secondly, I document native habitats that are not or unlikely to be invaded as well as noting any exotic Collembola that are not invasive although present in Australia. Their ecologies and traits where known are noted as well as those of the invaded on non-invaded habitats. Finally, I summarise this information and develop hypotheses on the characteristics of both invaded communities and invasive species based on this information.

2. Examples of invaded habitats

What factors facilitate invasion of exotic Collembola into exotic vegetation and prevent retention of natives?

2.1 Wheat crops

i) The soil and surface fauna of a tillage trial on broad-acre arable land in central New South Wales with seasonally dry summers and cool winters was sampled eight times over 20 years and all Collembola identified. Fertilisers and pesticides had been applied to the soil annually since 1990 when the trial began. Twenty-four species, mainly exotics, were found (Longstaff et al. 1997) and did not change significantly in composition between years but abundance varied with season and weather. In the early 1990s, there were a maximum of eight native species but, by 2017, only two native species, in very low numbers, were found, neither present in the 1990´s samples. The eight species lost were all epigaeic Symphypleona and Entomobryidae. (Greenslade & Nash in prep.) The differential effect on ecological types over time may be the result of an increased regime of spraying for aphids.

ii) The effect of herbicides on surface-active fauna was investigated in another tillage trial in broad-acre wheat paddocks also in central New South Wales in a locality with a similar climate. The fauna consisted of the same suite of exotic species of Collembola as the trial reported above and with the same four species of Symphypleona, one of which was native. Four exotic species were

Table 1. List of assumed exotic species of Collembola in Australia and their habitats in the country based on Greenslade & Ireson (1986) and later references by Greenslade 1987 to 2018. Species names in bold – abundant & widespread.

Superfamily	Family	Species	Definite	Probable	Misidentified	Habitat requirements
Entomobryomorpha	Entomobryidae	***Coecobrya communis* (Chen & Christiansen, 1997)**	D			disturbed land, caves, cattle grazed mound springs, logs, worm farms
Entomobryomorpha	Entomobryidae	*Coecobrya tenebricosa* (Folsom, 1902)	D			recently mining land, burnt plots, tropical
Entomobryomorpha	Entomobryidae	*Entomobrya albocincta* (Templeton, 1835)	D			single 1937 record Tasmania, now extinct?
Entomobryomorpha	Entomobryidae	*Entomobrya assuta* Folsom, 1924	D			imported timber, Barrow Island
Entomobryomorpha	Entomobryidae	***Entomobrya multifasciata* (Tullberg, 1871)**	D			exotic improved temperate grasslands, garden lawns, disturbed land, bare ground
Entomobryomorpha	Entomobryidae	*Entomobrya nigrocincta* Denis, 1924	D			straw, sub-clover, disturbed land
Entomobryomorpha	Entomobryidae	***Entomobrya unostrigata* Stach, 1930**	D			arable land, rye grass, sub-clover, domestic situations,
Entomobryomorpha	Entomobryidae	*Heteromurus major* (Moniez, 1889)	D			disturbed revegetated river banks, subtropical horticultural plantings
Entomobryomorpha	Entomobryidae	***Lepidocyrtus (Lanocyrtus) fimetarius* Gisin, 1964**	D			broad acre agriculture, fungal fruiting bodies, cotton fields, caves,
Entomobryomorpha	Entomobryidae	*Lepidocyrtus (Lepidocyrtus) violaceus* (Lubbock, 1873)	D			agricultural land, temperate
Entomobryomorpha	Entomobryidae	***Seira domestica* (Nicolet, 1942)**	D			domestic houses, sheds, garages
Entomobryomorpha	Entomobryidae	*Willowsia jacobsoni* (Börner) (Borner, 1913)	D			bark of tropical fruit trees
Entomobryomorpha	Entomobryidae	*Willowsia nigrofasciatus* Zhang & Pan		P		grain and other stores
Entomobryomorpha	Entomobryidae	*Willowsia plantani* (Nicolet, 1842)		P		under bark exotic trees
Entomobryomorpha	Isotomidae	*Ballistura schoetti* (Dalla Torre, 1895)	D			edge of unvegetated creeks, running fresh water, under stones
Entomobryomorpha	Isotomidae	*Desoria tigrina* (Nicolet, 1842)	D			suspect exotic plants, arable land, pasture
	Isotomidae	***Desoria trispinata* (MacGillivray, 1896)**				improved pasture
Entomobryomorpha	Isotomidae	***Folsomia candida* Willem, 1902**	D			caves, laboratory culture, bulbs
Entomobryomorpha	Isotomidae	*Folsomia similis* Bagnall, 1939	D			cattle grazed mound springs
Entomobryomorpha	Isotomidae	***Hemisotoma thermophila* (Axelson, 1900)**	D			warm, humid sites, disturbed or not
Entomobryomorpha	Isotomidae	*Isotoma viridis* Bourlet, 1939		P		suspect exotic plants, arable land, pasture
Entomobryomorpha	Isotomidae	*Isotomiella cribrata* Deharveng & Suhardjono, 1994		P		cotton fields
Entomobryomorpha	Isotomidae	*Isotomiella minor* (Schäffer, 1896)		P		soils
Entomobryomorpha	Isotomidae	*Isotomurus maculatus* (Schäffer, 1896)	D			suspect exotic plants, pasture, home gardens
Entomobryomorpha	Isotomidae	***Isotomurus palustris* (Müller, 1776)**	D			suspect exotic plants, pasture, home gardens
Entomobryomorpha	Isotomidae	*Isotomurus unofasciatus* (Börner, 1901)		P		improved pastures, humid sites
Entomobryomorpha	Isotomidae	***Parisotoma notabilis* (Schäffer, 1896)**		P		acid soils, low diversity
Entomobryomorpha	Isotomidae	*Proisotoma filifera* (Denis, 1931)	D			grazed pastures, moist warm compost

Superfamily	Family	Species	Definite	Probable	Misidentified	Habitat requirements
Entomobryomorpha	Isotomidae	***Proisotoma minuta* (Tullberg, 1871)**	D			temperate climates, disturbed habitats. compost, bulbs, indoor plants, fungal fruiting bodies, cotton fields
Entomobryomorpha	Isotomidae	*Proisotoma ripicola* Linnaniemi, 1912		P		fertilised seeded cleared land
Entomobryomorpha	Isotomidae	*Proisotoma tenella* (Reuter, 1895)	D			hot houses, one old record only
Entomobryomorpha	Tomoceridae	*Pogonognathellus flavescens* (Tullberg, 1871)	D			cultures, botanic gardens
Entomobryomorpha	Tomoceridae	*Tomocerus vulgaris* (Tullberg, 1871)	D			domestic gardens, southern
Poduromorpha	Brachystomellidae	*Brachystomella cyanea* (Rapoport, 1962)	D			agricultural land, temperate climates
Poduromorpha	Brachystomellidae	***Brachystomella platensis* Najt & Massoud, 1974**	D			moisture, low temperatures, arable land or exotic grasses, fungal fruit bodies
Poduromorpha	Hypogastruridae	***Ceratophysella communis* (Folsom, 1898)**	D			pastures, pine forest, cattle dung
Poduromorpha	Hypogastruridae	***Ceratophysella denticulata* (Bagnall, 1941)**	D			moisture, cool temperatures, labile nutrients, improved pastures, fungal fruit bodies
Poduromorpha	Hypogastruridae	***Ceratophysella gibbosa* (Bagnall, 1940)**	D			moisture, cool temperatures, labile nutrients, arable land, caves
Poduromorpha	Hypogastruridae	*Hypogastrura assimilis* (Krausbauer, 1898)		P		rare, warmer climates, leaf litter
Poduromorpha	Hypogastruridae	*Hypogastrura distincta* (Axelson, 1902)	D			one record compost heap
Poduromorpha	Hypogastruridae	***Hypogastrura manubrialis* (Tullberg, 1869)**	D			only disturbed land, moist, cool temperatures, labile nutrients, fungal fruiting bodies
Poduromorpha	Hypogastruridae	***Hypogastrura purpurescens* (Lubbock, 1867)**	D			very cool temperatures, labile nutrients, high levels of moisture, temperate rainforest leaf litter, fungal fruiting bodies
Poduromorpha	Hypogastruridae	*Hypogastrura succinea* (Gisin, 1949)	D			one record, garden
Poduromorpha	Hypogastruridae	***Hypogastrura vernalis* (Carl, 1901)**	D			moisture, cool temperatures, labile nutrients, arable land, improved pastures
Poduromorpha	Hypogastruridae	***Hypogastrura viatica* (Tullberg, 1872)**	D			saline, periodically flooded
Poduromorpha	Hypogastruridae	*Mesogastrura libyca libyca* (Caroli, 1914)	D			caves, moist situations
Poduromorpha	Hypogastruridae	*Xenylla grisea* Axelson, 1900	D			exotic vegetation, moderate temperatures, low humidity
Poduromorpha	Hypogastruridae	*Xenylla humicola* (Fabricius, 1780)			M	n. a.
Poduromorpha	Hypogastruridae	*Xenylla maritima* Tullberg, 1869	D			under bark of *Pinus radiata*, marine littoral
Poduromorpha	Hypogastruridae	*Xenylla mucronata* Axelson, 1903	D		M	probably incorrect identification
Poduromorpha	Hypogastruridae	*Xenylla yucatana* Mills, 1938	D			saline tolerant, tropical sites, moist
Poduromorpha	Neanuridae	*Anurida granaria* (Nicolet, 1847)	D			moist soil, gardens, under stones, beside temperate creeks
Poduromorpha	Neanuridae	*Blasconura hirtellus* (Börner, 1906)			M	one record only, tropical island, near Indonesia
Poduromorpha	Neanuridae	***Friesea claviseta* Axelson, 1900**	D			leaf litter of coconut, bananas, nursery soil
Poduromorpha	Neanuridae	*Friesea mirabilis* (Tullberg, 1871)		P		on bulbs, garden soil

Superfamily	Family	Species	Definite	Probable	Misidentified	Habitat requirements
Poduromorpha	Neanuridae	*Micranurida* sp.			M?	n. a.
Poduromorpha	Neanuridae	*Neanura muscorum* (Templeton, 1835)	D			acid soils, arable land, leaf litter of exotic plant, caves
Poduromorpha	Odontellidae	*Odontella lamellifera* (Axelson, 1903)		P		unknown check records
Poduromorpha	Onychiuridae	Cf *Thalasaphorura encarpata* (Denis, 1931)				urban soils, compost
Poduromorpha	Onychiuridae	*Deuteraphorura inermis* (Tullberg, 1871)	D			moist, exotic vegetation
Poduromorpha	Onychiuridae	*Onychiurus ambulans* (Linnaeus, 1758)		P	M?	n. a.
Poduromorpha	Onychiuridae	***Orthonychiurus folsomi*** **(Schäffer, 1900)**	D			warm temperatures, high levels of nutrients, worm cultures, caves
Poduromorpha	Onychiuridae	***Protaphorura fimata*** **(Gisin, 1952)**	D			agricultural land, roots, seeds
Poduromorpha	Tullbergiidae	*Mesaphorura baconae* Bagnall, 1947				temperate pasture soil, agricultural land
Poduromorpha	Tullbergiidae	*Mesaphorura critica* Ellis, 1976		P		one record, arid soils
Poduromorpha	Tullbergiidae	***Mesaphorura macrochaeta*** **Rusek, 1976**	D			low competition sites, soil, arable land
Poduromorpha	Tullbergiidae	*Mesaphorura yosii* (Rusek, 1967)	D			low competition, soil, arable land
Poduromorpha	Tullbergiidae	*Metaphorura affinis* (Borner, 1902)	D			polluted soils, exotic grasses
Poduromorpha	Tullbergiidae	*Stenaphorura quadrispina* (Börner, 1901)				soil
Symphypleona	Bourletiellidae	***Bourletiella hortensis*** **(Fitch, 1863)**	D			green crops
Symphypleona	Bourletiellidae	***Bourletiella viridis*** **Stach, 1920**	D			green crops
Symphypleona	Bourletiellidae	*Deuterosminthurus flavus* (Gisin, 1946)		P		exotic grass, pastures, mediterranean climates
Symphypleona	Bourletiellidae	*Deuterosminthurus sulphureus mediterraneus* Ellis, 1966	D	P		exotic grass, pastures, mediterrean climates
Symphypleona	Bourletiellidae	*Fasciosminthurus quinquefasciatus* (Krausbauer, 1898)				temperate improved pastures
Symphypleona	Bourletiellidae	*Fasciosminthurus virgulatus* (Skorikow, 1899)	D			exotic grass, pastures, temperate sites
Symphypleona	Bourletiellidae	*Pseudobourletiella spinata* (MacGillivray, 1893)	D			surface of fresh water, still
Symphypleona	Dicyrtomidae	*Ptenothrix vittata* (Folsom, 1896)		P		hot house
Symphypleona	Katiannidae	*Sminthurinus aureus* (Lubbock, 1862)		P		widespread southern moist habitats
Symphypleona	Katiannidae	***Sminthurinus elegans*** **(Fitch, 1863)**	D			exotic grass, pastures, temperate climates
Symphypleona	Katiannidae	*Sminthurinus igniceps* (Reuter, 1881)	D			greenhouses, quarantine facilities
Symphypleona	Katiannidae	*Sminthurinus mime* (Börner, 1907)		P		arable land
Symphypleona	Katiannidae	*Sminthurinus niger* (Lubbock, 1868)		P		widespread southern moist habitats
Symphypleona	Katiannidae	***Sminthurinus quadrimaculata*** **(Ryder, 1879)**	D			greenhouses
Symphypleona	Sminthuridae	***Sminthurus viridis*** **Linnaeus, 1758**	D			exotic grass, pastures, mediterranean climates
Symphypleona	Sminthurididae	*Sminthurides aquaticus* (Bourlet, 1843)	D			fresh water, disturbed sites
Symphypleona	Sminthurididae	*Sminthurides malmgreni* (Tullberg, 1877)		P		rare, cool greenhouse, moss
Symphypleona	Sminthurididae	*Sphaeridia boettgeri* Bretfeld & Gauer, 1994	D			cotton fields
Symphypleona	Sminthurididae	***Sphaeridia pumilis*** **(Krausbauer, 1898)**		P		widespread temperate leaf litter
Symphypleona	Sminthurididae	***Stenacidia violacea*** **(Reuter, 1881)**	D			temperate arable land

significantly affected adversely in the short term by the herbicide, including one Symphypleonan, but the native species, *Katianna australis*, did not appear to be affected. (Greenslade et al. 2010). This result is contrary to predictions as it suggests the native species were not affected by the characteristics of the highly modified wheat field while the exotic species were.

2.2 Cotton crops

In 1995, soil animals were sampled in cotton paddocks in northern New South Wales at different times after clearing native vegetation or converting from pasture to wheat. The climate is a local steppe type with hot summers, coolish winters and low rainfall. The collembolan fauna was low in diversity as only 23 species were collected, mainly exotics. The 'youngest' site, which had only been converted to cotton one year previously, carried 16 species while the oldest site, which had been carrying cotton for 25 years, carried only five species (Lytton-Hitchins et al. 2015). The most abundant species, the exotic *Entomobrya unostrigata*, was tolerant of wet/dry conditions and of chemical applications (Greenslade 1995). Again, all the losses were of Symphypleona, including six species on the 'youngest' site of which at least three, possibly four, were native. Adjacent native vegetation carried nearly all native species (5 out of 15 were exotic) (Lytton-Hitchins et al. 2015).

2.3 Improved pasture

Increasing levels of fertiliser was applied to three native pasture locations in South East Australia, carrying predominately *Danthonia* species. Both epigaeic and soil living Collembola were affected by the treatment. Some native species were eliminated at high levels of fertiliser, while exotic species were favoured (Oliver et al. 2005). Fertiliser application and grazing increased the relative abundance of introduced Collembola.

2.4 *Chysanthemoides monilifera*

The South African *Chrysanthemoides monilifera* ssp. *rotundata* (DC.) T.Norl. (bitou bush) has invaded wide strips of south-east coastal Australia. Leaf litter bags placed under both bitou bush and in native vegetation showed that *C. m. rotunda* leaves decomposed three times faster than the native *Acacia, Banksia and Leptospermum* leaves, indicating that they were more palatable. Soil nitrogen was higher on invaded sites and it was cycled faster, significant as it has been shown elsewhere that higher nitrogen levels are associated with higher numbers of exotic species and fewer natives. Analysis of collections of leaf litter invertebrates beneath bitou bush and from native vegetation showed that the bitou bush changed the abundances of some crustacean invertebrates. The changes were attributed to a different moisture content of leaf litter under *C. m. rotundata* (Lindsay & French 2006). The changed nutrient content also may have caused the differences in faunal abundances. This project failed to distinguish between exotic and native Collembola but did suggest that a characteristic of exotic plant invasion is a high level of leaf litter moisture.

2.5 *Olea europaea* L.

Leaf litter invertebrates were sampled in southern New South Wales in a botanic garden and adjacent exotic olive groves of various ages. As with the other plants of a Mediterranean climate origin, such as the bitou bush, changes in abundance were noted in some invertebrate taxa (Nguyen et al. 2016). Total Collembola were more abundant in the ecotone between the olive orchard and native forest than in either the orchard of the forest. This is another example of a project that would have benefited if native and exotic species had been distinguished but shows that exotic plants alter Collembola communities.

2.6 *Pinus radiata* D. Don var. *binata* plantations

Invertebrates were collected from leaf litter taken from a 20-year-old exotic pine plantation and adjacent native undisturbed *Eucalyptus* woodland in south east South Australia. Over 95 % of the fauna of the pine plantation comprised the exotic species *Xenylla maritima* Tullberg, while less than 1 % of the fauna from the native eucalypt litter consisted of exotics (Howard & Greenslade 1985). At another pine plantation site nearby, collembolan numbers were high due to the dominance of three exotic species: *Ceratophysella* sp. and two acidophilic species, *Mesaphorura* sp. and *Parisotoma notabilis*. The mean pH at these two sites was 4.75.

2.7 *Solidago gigantean* L.

In a European study, the soil properties, in particular the pH of wet meadows was significantly changed by the invasion of this weed. At the same time Collembola community composition, but not abundance was changed. As this study was in Europe, there are no distinctions between exotic and native species as all species are invaders after the retreat of glaciers. Sterzynska et. al (2017) listed seven species, of which four are invasive in Australia, which were significantly more abundant in invaded sites and seven, of which again four are invasive in Australia, that were more abundant on uninvaded sites. These results illustrate how the threats posed by invasive species are unique to Australia.

3. Comparison of invaded/ non-invaded habitats

3.1 Invasion of exotic Collembola into exotic vegetation

Collembola were collected four times a year from a grazing trial in northern NSW using three stocking rates in each of two types of grassland, native *Themeda* with *Poa* in contrast to exotic fertilised pastures carrying *Phalaris* and *Trifolium*. Native species of Collembola dominated the native pasture in numbers of species present (19 natives compared to 11 exotics) and in abundance, while introduced Collembola dominated fertilised exotic pasture (16 exotics compared to nine natives) and this difference was statistically significant (King et al. 1985). The species that were restricted to a single pasture type were mainly native, species in native grassland or exotic species in exotic grassland. Both types were epigaeic and hemiedaphic species. The abundance of introduced Collembola was positively associated with phosphorus content of leaf litter (King et al. 1985). This suggests that exotic species invasions were facilitated by the change in phosphorus and the reverse for native species.

3.2 Fungal fruiting bodies

Thirty-one species of Collembola were collected from 36 fungal fruit bodies in native forest in south east Australia. The fungi belonged to 20 genera (PG unpublished data). Not all fungal genera were colonised by Collembola. *Mycena, Cladosporium, Hymenogaster* and *Psillosopha* species hosted Collembola, while *Ganoderma* did not. Other genera were too rare for data to be reliable. Considering the total collection, sixty-five per cent of the Collembola collected were introduced hypogastrurids. A test in native forest comparing the colonisation of native fungi with the exotic *Agaricus bisporus* (Lge.) Sing, commercially sourced was set out in native forest, ten samples of each. Only exotic but not native Collembola colonised the exotic *Agaricus*, while alternatively the introduced hypogastrurids also colonised the native fungi. There was a significant suppression of numbers of each native species in native fungal fruiting bodies when hypogastrurids were present (Mann-Whitney test $p < 0.001$), while abundance of native species in the same samples had less effect on numbers of exotic species (Mann-Whitney test $p < 0.05$). These hypogastrurids, all exotic species, appeared to have a competitive advantage over the native species, at least on fungi.

3.3 Restoration sites

In an attempt to measure the effect of restoring native vegetation to disturbed sites, 21 sites (nine with remnant vegetation, six revegetated and six cleared and with only exotic grasses) were sampled for Collembola. Exotic species of Collembola (*Hypogastrura* and *Ceratophysella*) were dominant on sites lacking native vegetation and their abundance was statistically significantly related to the density of exotic grasses ($r = 0.60$, $p < 0.05$) (Greenslade et al. 2011). Remnant native vegetation rarely carried exotic Collembola.

4. Invasion of exotic Collembola into native vegetation

4.1 Grampian Ranges

This extensive mountain range has been little disturbed by human activities except by localised foot traffic. It has never been extensively surveyed for Collembola, but sparse collections from native vegetation indicate it carries a diverse native and endemic fauna. The range has, however, been subject to extensive wildfires leading to loss of vegetation. Fires have sometimes been followed by heavy rain, causing considerable soil erosion. A non-indigenous *Acacia* species, *A. longifolia longifolia,* (Andrews) Willd., originally from northern New South Wales, has invaded parts of the range from 1999 onwards, mainly along creek lines after fire (M. Stevens 2018, pers. comm., Adair 2008, Richardson & Kluge 2008). *Acacia l. longifolia* is known for being a highly invasive species (Foreman & Walsh 1993) with detrimental impacts on ecosystems (Richardson et al. 2000, Adair 2008, Richardson & Kluge 2008, Marchante 2011). Impacts include accelerated biomass accumulation, reduced light penetration, increased nitrification, changed fire intensity and frequency, altered geo-morphological processes and hybridisation with congeners (Adair 2008).

Invertebrates were collected from both beneath the exotic *Acacia* and the indigenous *Acacia mearnsii* De Wild. and other native shrubs in order to detect changes in species composition. Leaf litter was deeper and moisture content greater under *A. l. longifolia* compared to native shrubs and the invertebrate fauna differed in that two exotic species, a Collembola, *Hypogastrura vernalis* and a cockroach were more abundant under the introduced *Acacia* species (Adin James 2017). Leaf litter depth and moisture content were positively correlated with numbers of *H. vernalis* and immature unidentified cockroaches (Adin James 2017) (Tab. 2). No cockroaches were found under the native vegetation and few Hypogastruridae (see Tab. 2). The physical changes in the native vegetation caused by the invasive *Acacia* must have been considerable for such large changes in the fauna to have occurred. It is suggested that a combination of higher moisture content, and absence of decomposers adapted to colonise the invasive *Acacia* leaf litter were at least partially the cause.

4.2 Dandenong Ranges

Extensive collections of Collembola have been made in the Dandenong Ranges, Victoria, in areas of native vegetation in 2015. The Dandenong Ranges is located near but south east of Melbourne. It is a complex area of valleys and low hills covered in thick temperate rainforest and dense ferny undergrowth. Although protected it is affected by low impact recreation. No exotic Collembola were found apart from one site of about 100 m^2, where *Orthonychiurus folsomi* dominated collections (P. Greenslade, unpublished data). This site did not appear to differ floristically from other sites in the vicinity that did not have onychiurids present, but it was closer to a footpath and road (N. Porch pers. comm. 2018).

4.3 Tasmanian t Temperate rainforests

Exotic species were rarely found during invertebrate surveys of 12 sites in Tasmanian temperate rainforests in 1990 and 1991. However, at one site, near Projection Bluff, Central Plateau, the exotic *Hypogastrura purpurescens* was found dominating the fauna. This site was close to a road. In another small patch of native *Nothofagus* in the north east region, 20 km south east of Scotsdale, a locally endemic Collembola genus (and species), *Tasphorura vesiculata* Greenslade and Rusek, 1996, was dominant in moss (Coy et al. 1993). However, this species was not found in 2011 over fifteen years later and it appeared to have been replaced by the exotic *H. purpurescens*, which now numerically dominated the ground layer. The dense mossy ground layer present in the early 1990s had disappeared which was the habitat of *T. vesiculata*. The reason for this could be two-fold. In the intervening 13 years, the original native *Eucalyptus* forest that surrounded the rainforest had been cleared and replaced by plantations of *E. globulus* Labill. Extensive vehicle activity had also taken place around the rainforest patch and there was a track for trucks around it, thereby increasing penetration of edge effects especially light. This, together with a lowering of rainfall and increase in temperature, had resulted in a drying of the ground layer, with deleterious effects on the original fauna. The change in habitat facilitated the invasion of the exotic Collembola.

4.4 Subantarctic Islands

Macquarie Island

The fauna of Macquarie Island consists of 37 (22 native/indigenous) collembolan species, of which 15 are exotics (Greenslade 2006). The exotic species are almost entirely confined to the coastal strip around the island, which carries indigenous vegetation. Two of the numerically dominant exotic species are the cosmopolitan hypogastrurids, *Hypogastrura viatica* and

Table 2. Abundance of Blattodea, *Hypogastrura vernalis* and leaf litter depth at invaded and non-invaded sites in the Grampian Ranges.

	Native vegetation Jan	Invaded sites Jan	Native vegetation Feb	Invaded sites Feb	Native vegetation Mar	Invaded sites Mar
Leaf litter depth in cms	trace	90, 130, 155	trace	90, 130, 150	trace	100, 140, 145
Abundance of Blattodea	0	25, 30, 40	0	10, 22, 20	0	15, 25, 30
Abudundance of *Hypogastrura vernalis*	29, 34, 44	508, 3319, 3430	13, 18, 23	324, 1524, 1826	19, 27, 38	573, 704, 802
Moisture content %	7, 8, 9	9, 10, 11	6, 6, 7	9, 9, 9	5, 5, 6	7, 7, 7

Ceratophysella denticulata. The latter species is confined largely to areas of the native cabbage, *Stilbocarpa polaris* (Hombr. & Jacquinot ex Hook.f.) A.Gray, a soft leaved, rapidly decaying plant with minimum leaf litter accumulation. No exotic species were found in the more severe climate of the plateau up to 2012. The other 13 exotics are generally found near sites of human activity and are mainly soil living (Greenslade 2006). There is evidence that some of these exotic species are expanding their range into native environments (Greenslade et al. 2008). None of the other plants, such as mosses on the island, harboured exotic species, but the single exotic invasive plant present, *Poa annua*, L. has not been sampled (Williams et al. 2018, Greenslade 2006).

South Georgia

Only *H. viatica* was present on this island (Wise 1970) until exotic weeds were inadvertently introduced around the few dwellings on the island (Convey et al. 1999). Collections from around the settlement made firstly in 1999 found one additional exotic species and in 2005 and later, a further three exotic species were collected. These were only found associated with exotic plants that had colonised a small area near now unused huts (Greenslade & Convey 2012). It was suggested that the importation of root and other vegetables was the route by which these species arrived and colonised the island (Greenslade & Convey 2012).

Deception Island in the South Shetland

This island in the South Shetlands is heavily visited by tourists. Six exotic species are known from the island, all in areas visited by large groups of tourists on a daily basis over summer. Several exotics species are only found near geothermal vents (Greenslade et al. 2012).

4.5 Sub-alpine grasslands open herbfields

The Mt Stirling ski resort and the surrounding land are used for recreational activities such as horse trekking, skiing and other off-track human activities throughout the year. The vegetation comprises a herbfield/grassland interspersed with low shrubs (McDougall & Walsh 2007). Analysis of pitfall catches from Mt Stirling, Victoria, on a disturbed area, near a road, on the west-southwest-face of the summit, showed that the exotic species, *Ceratophysella gibbosa* was dominant. This species was absent from five other montane sites also sampled with pitfalls, but these five were undisturbed and not developed for tourism or recreational activities (Greenslade & Slatyer 2017).

5. Native ecosystems, vegetation types and localities less or not vulnerable to exotics

5.1 Arid and semiarid lands

Control of locusts using insecticides, in this case Fenitrothion, was the chemical spraying regime carried out in extensive areas of native vegetation in arid Australia. A trial was undertaken at a site near Broken Hill, northwest New South Wales, and invertebrates were trapped in pitfalls before and after spraying for six weeks in native grassland. Twenty species of Collembola were collected, all native. Lower numbers of entomobryids were collected in sprayed areas. It appears that no exotic Collembola from other arid lands, i.e. from parts of Africa and Central Asia, have been introduced to Australia and established in arid parts of the continent.

5.2 Coastal and montane heathlands, moorland, tundra

Serendipitous collections from a number of these ecosystems and vegetation types over time have failed to detect any exotic species. It is possible that the nutrient contents of these soils, known to be exceptionally low, do not provide favourable habitat for the exotic species that have colonised ecosystems with soils higher in nutrients in Australia (P. Greenslade unpublished results).

5.3 Tropical rain forests

No exotic species have been found dominating these vegetation types. The high temperature is probably not suitable for exotics from Europe. *Orthonychiurus folsomi* is found sporadically in warmish climes such as Central Asia (Qazi & Shayan 2016). It is a species most abundant and tolerable of high nutrient and high temperature habitats such as worm beds (P. Greenslade unpublished results). Its ecological preferences have allowed it to colonise moist forest on subtropical off shore eastern islands but not mainland forests, probably introduced by visitors. Perhaps competition or predators are reduced there (P. Greenslade unpublished report 2018).

5.4 Marine littoral, sand dunes and fresh water aquatic habitats

One different exotic species has invaded each of these four ecosystems in southern regions of Australia. The apparently near ubiquitous *H. viatica* has invaded many southern marine littoral habitats and saline swamps, including some inland lakes (Lake Coolac). The species has not been found further north than New South Wales nor under mangroves (Greenslade et al. 2014). Sand dunes, subject to extreme fluctuations of temperature and moisture have been colonised by *Seira domestica*, a species commonly found in dwellings. The surface of static fresh water bodies has been colonised by both *Sminthurides aquaticus*, and rivers by *Pseudobourletiella spinata*. All four of these species are cosmopolitan in distribution, but restricted as to habitat type (Greenslade 2018).

5.5 Lord Howe Island

Exotic species were rare in collections made on four occasions in the early 2000's (P. Greenslade unpublished results). *Hypogastrura denticulata* and *H. purpurescens* were sporadic and only in low numbers. *Orthonychiurus folsomi* was only found abundantly on one site.

5.6 Norfolk and Philip Islands

Both islands were surveyed for invertebrates during the 1980s and some species records for them published. The collembolan fauna was moderately rich, being estimated at around 50 species including two that are endemic. However, the faunas of both islands were on some sites dominated by exotic species, both soil and epigaeic species, especially on moister sites with native vegetation. *Orthonychiurus folsomi* and a single *Ceratophysella* species dominated some collections on Norfolk Island. The only collections where these two species were absent were from a minute precipitous offshore island, Lion Rock. A quarter of the species found on Philip Island were exotics, although they were absent from the drier sites. The high numbers and widespread occurrence of exotic species on Norfolk Island is probably the result of extensive disturbance by humans and livestock over many years as well as the equable warm moist climate (P. Greenslade unpublished report).

6. Exotic plants/weeds not invaded by exotic Collembola

It might be expected that all invasive exotic plant species would be ideal hosts for exotic Collembola because they spread rapidly, form large swards, many have soft, rapidly decaying leaves and can tolerate a variety of conditions. *Cenchrus ciliaris,* L., the exotic buffel grass originating in the Middle East, was introduced to central Australia over a century ago and has now spread widely in the region, particularly along creek lines is an exception. Sporadic collections have contained no exotic Collembola, however a highly impoverished fauna. Native grasses in the region carry up to seven species of the endemic genus, *Corynephoria,* but only one widespread *Corynephoria* species has been found on buffel grass and then only in low numbers (P. Greenslade unpublished results).

7. Non-invasive exotic species of Collembola

Exotic species vary in their reproductive capacity and dispersal ability. The list of exotic species that are in Australia (Tab. 1) includes a number of species with few records, but these tend to have specialised habitat requirements such as fresh water, creek banks, marine littoral habitats and urban situations. They may have a high reproductive capacity and/or occur in such restricted habitats that they have been rarely collected.

8. Native species in modified disturbed habitats

The examples given above suggest that exotic habitats are hostile to native species and so they are a conservation threat. Although true for most native species, that is not true of all and some examples are given below. Greenslade & Ireson (1986) list a number of native species that are able to live in improved pastures of mixed native and exotic grass species. These authors list seven *Katianna* species in Tasmania, of which *Katianna australis* is the most frequently encountered. The species *C. reticulata* of the endemic genus *Corynephoria* is another example. It has been recorded from dam sites in the arid zone and cropping fields in Western Australia. The primary coloniser of mined and restored sites in Western Australia is a species of the native genus *Acanthomurus*. McDonald & Rodgers (2010), in a survey of invertebrates of agricultural land under both pasture and crops, recorded no native species, although they did not identify beyond genus. It appears however that native Australian species cannot persist in broad acre agricultural land, but that some species can tolerate improved pasture.

9. Discussion

Although none of the surveys quoted here were carried out with the aim of determining what habitat factors were responsible for facilitating invasion by exotic Collembola, taken together they strongly suggest that disturbance from the original natural state, such as evident in broad acre agricultural land, improved pastures, cropping fields and exotic plantations, are the most vulnerable. By way of contrast, native species are nearly always restricted to native environments. These disturbed habitats vary in their susceptibility to invasion and as to which species will be able to colonise them. Prins & Gordon (2014) asked twelve plant and vertebrate biologists which of 11 characteristics of habitats were relevant as to vulnerability of invasion by their group. Only one received majority support, that of disturbance. Others related to abiotic conditions, competitors, predators, empty niches, resource limitation in the habitat or if the species was *r* selected were not supported. Invertebrates were not included.

Exotic species found in Australia belong to nearly all families. For instance, the Paronellidae and Spinothecidae do not have exotic species in Australia, the Sminthurididae are a small family with few total species recorded but several are exotic, and no exotics in the families Oncopoduridae, Neelidae and Arrhopalitidae have been detected. To illustrate these differences, the family composition of exotic species is shown in Figure 1 as a percentage of total number of species known in Australia in that family. Most families have just over 20 % of recognised species classified as exotics. The high numbers of exotics and absence of endemic species in the families Onychiuridae and Hypogasturidae indicate that the evolutionary history of these families differs from those families composed largely of endemic species. There are no endemic Australian species of Onychiuridae, and native species are known in only four of nine genera of Hypogastruridae. This suggests that these families may have diversified partly at least on the current Northern Hemisphere continents and not on any current Southern Hemisphere continents.

In table 3, 11 characteristics that are present in habitats that have been invaded by exotics are listed as present or absent in 11 of the land types treated above. Presences are summed. The most frequently recorded vulnerability is presence of exotic grasses and weeds (score 9) and then total loss of native vegetation (score 8, Tab. 3), and lesser

Table 3. Abiotic and biotic factors of habitats that facilitate invasion of exotic Collembola.

Ecosystem/ Vegetation type	Pesticides	Fertilisers	Deep leaf litter	Exotic grasses/ weeds	High moisture	Cool temperatures	Trampling/soil compaction	Total loss of native vegetation	Competition low	Predators low	Edge effect
Wheat crops	+	+	-	+	-	-	+	+	+	+	+
Cotton crops	+	+	-	+	-	-	+	+	+	+	+
Improved pasture	+	+	-	+	-	-	+	+	-	-	-
Chrysanthemoides sp. infestation	-	-	+	+	-	-	-	+	-	-	-
Olea europaea infestation	-	-	-	+	-	-	-	+	-	?	?
Acacia l. longifolia infestation	-	-	-	+	+	+	-	+	-	+	-
Pinus radiata	-	+	+	+	-	-	-	+	-	+	-
Stilbocarpa polaris	-	-	-	-	+	+	-	-	-	-	-
Fungal fruiting bodies	-	-	-	+	-	-	-	-	+	+	?
Exotic grasses (Dandenong Ranges)	-	-	+	+	+	+	-	+	-	-	-
Temperate rainforests	-	-	+	-	+	+	-	-	-	-	-
Montane grassland (Mt Stirling)	-	-	-	-	+	+	-	-	-	-	-
Total / Score	**3**	**4**	**5**	**9**	**5**	**5**	**3**	**8**	**3**	**5**	**2**

vulnerabilities are deep leaf litter, cool temperatures low predators and high moisture (all score 5). Other factors not able to be evaluated, as only limited data is available, are high nutrient levels, changed soil microbial community and simplified habitat structure. The vegetation type with most adverse characteristics is broad acre agricultural crops (Tab. 3).

Species traits

Identification of Collembola to species instead of only class or family, has allowed a comparison of the abundances of exotic with native species in different surveys. As the ecologies of the exotic species are known from their native distributions, their species traits are known and this permitted in some cases an

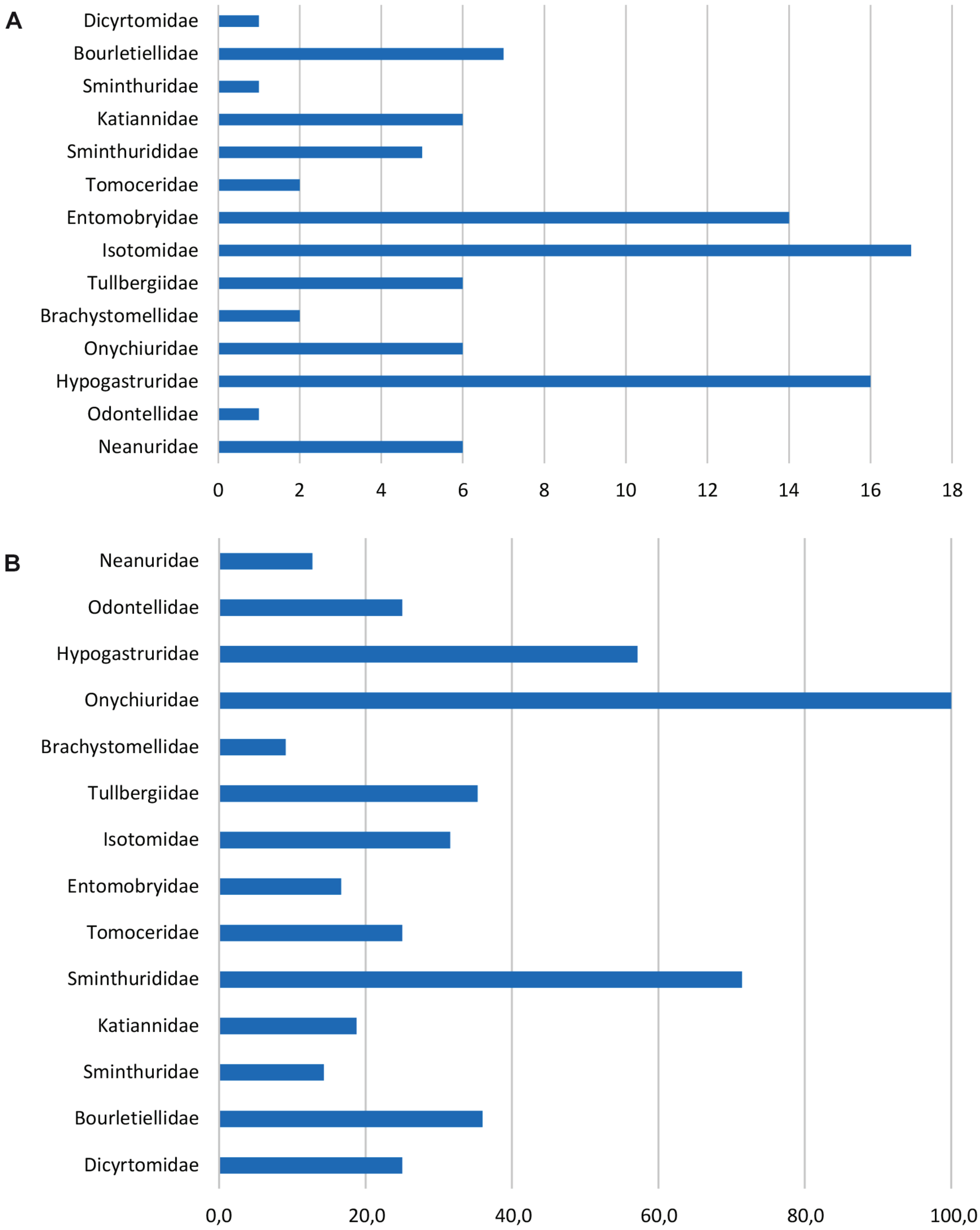

Figure 1. (**A**) Number of exotic species in each Collembola family occurring in Australia, (**B**) Percentage of exotic species of total species in each family in Australia.

estimation of the risk of further invasions under a warming climate scenario. Table 1 summarises the main habitat requirements of each exotic species and demonstrates that they differ widely. Assessing each species according to ecological traits and plotting the summed traits using the habitat templet (Greenslade & Greenslade 1973) has allowed the risk of invasion into different locations to be quantified. For instance, collembolan traits were used to measure how much intensity of grazing increased habitat vulnerability to exotics (King et al. 1985, Greeenslade 2007). Traits were also used to construct a risk assessment to guide quarantine management for Heard Island (Greenslade 2002). The scheme was further developed for South Georgia (Greenslade & Convey 2012), as the risk assessment needs to be specific to each location. A more limited range of species traits, morphology only, were used to predict composition of different communities (Salmon & Ponge 2012) in an attempt to model species associations with habitat characteristics at a small scale in a forest near Paris, France. These authors did not include ecological or distributional characters of the species in their model. As the European species cannot be grouped separately into native and exotic species, unlike in Australia, it was not possible to find a trait that clearly separated species. The results from this French study were equivocal.

As illustrated in Table 1, exotic species vary widely in their habitat preferences so it is not possible to predict which species are the most invasive overall for all habitats. Instead, the approach must assume *a priori* that the exotics in Australia all tend to be *r* selected. The application of the correlates of this strategy as, listed by Greenslade (1983), where it was described can be applied to determine which species are exotic in Australia. They are as follows: high rate of population increase, short life history, highly vagile, wide distribution, low specialisation and highly favourable but variable preferred habitats. Australian exotic species may possess some, but not all of these traits. There have been attempts to correlate temperature tolerance to the ability of collembolan species to adapt to climate warming and, as a correlate, to relate this to invasion success now and in the future (Janion-Scheepers et al. 2017). Testing a single trait is unlikely to be widely applicable especially if second generation, polyvalent cultured individuals are used as models because physiological character can be modified in culture. Other unpredictable features of novel environments that are likely to influence invasion success are competition, both indirect and direct, but difficult to measure. One example was described by Greenslade et al. (2002), where exotic species outcompeted native species on fungal fruiting bodies.

A method of assessing risks using a combination of morphological, biogeographical, ecological and biological traits rather than a single one was described by Greenslade (2002) for subantarctic Heard Island and South Georgia (Greenslade & Convey 2012) as noted above. No exotic species have so far been recorded from the first island except for a thrips (Green & Mound 1994) and the assessment indicated that three species of hypogastrurids had the highest risk of invading the island. For South Georgia, two hypogastrurids, one isotomid, one entomobryid, one onychiurid and one Neelipleona had a high invasive risk. These species are the same as those invading southern regions of Australia (Greenslade et al. 2012). A risk assessment for exotics colonising subtropical Barrow Island has also been developed using the same method (Supplementary file S1). Only one species, an entomobryid, has been shown to have recently invaded this island, but three other species had a high risk of being introduced. They were all entomobryid species that are regularly found in dry, warm habitats such as houses, factories and garages.

A confounding factor which makes predictions about which species could be invasive problematic when introduced to a new region, is that some exotic species in Australia identified as a European species, have been shown, using molecular data, to be composed several lineages in morphological identical populations (Porco et al. 2012). None of the lineages forms large populations in Europe, while they do in Australia (Fjellberg 1998, 2007). The reason for this is obscure but may be due to release from competitor and predatory pressure.

Vulnerable habitats

The vulnerability of ecosystems, on the evidence presented in this review, appears to be determined by the nutrient and moisture status of the soils. This is illustrated in Table 3 where the different types of disturbance inflicted on each habitat surveyed in Australia are listed. A change in nutrient status can be caused by a change in the composition of *Acacia* species present, as they are among the most invasive plants worldwide. Hellmann et al. (2011) found *A. l. longifolia* invaded dunes in Portugal and substantially impacted community plant structure, soil properties and growth rates of native species as well as decreasing biodiversity. Human intervention such as fertiliser application containing phosphorus, can threaten native biodiversity by facilitating invasion by exotic plant species (Driscoll & Strong 2017). These authors' nutrient enhancement trials produced variable results, but high values tended to favour exotic over native plants, which were modified by grazing (Driscoll & Strong 2017). Similarly, reducing phosphorus content and increasing grazing can reduce invasion pressure from weeds

(Thomas 2005). A recent burn can increase nutrient status as well because of the potash produced. Invasive Collembola such as *Hypogastrura vernalis* seem to be dependent on high potassium soils as Watson et al. (1982) showed in a study of its chemical composition body that it contained an unusually high content of potassium. Also, Oliver et al. (2005) showed that exotic Collembola are associated with high phosphorus and potassium.

Resistant habitats

Examples of Australian habitats resistant to invasion are the undisturbed low nutrient soils of much of Australia, especially native grasslands. Ecosystems that experience high temperatures, such as tropical rainforests, also seem resistant, probably due to most exotic Collembola originated in cold temperate climates. However, ecosystems in some low temperature, moist but otherwise severe locations are also apparently resistant, such as the anaerobic soils in tundra that are of low nutrient status.

10. Conclusions

Although Australia has in place stringent protection measures against invasions via quarantine and inspections, the risk of breaching borders cannot be totally eliminated. For example, the number of exotic species in general continues to increase (Rural News 2017). Exotic springtails have and are still being accidentally introduced to Australia in a range of imported commodities, most frequently in fruits, vegetables and timber. Wind, water and movements of animals are other modes of dispersal to Australia, being uncontrollable and unpredictable events (Parnikoza et al. 2018). Once having breached the borders, a species needs to establish, reproduce and spread for any impacts to be detected. Efforts put into surveillance and inspection are less costly than those of repairing environmental and economic damage (Greenslade et al. 2013).

Tabassum & Leishman (2016) suggested that only certain traits determined interactions between native and exotic species, but I show here that no single one determines success. Rather the combination of species traits, disturbance, qualities and vulnerabilities of ecosystems determine outcomes. Increased leaf litter depth, moisture content and insulation are not the only reasons for exotic Collembola preferentially forming large populations under certain plants, but that, high soil nutrient levels and resultant microbial population composition appear to be important. These characteristics are not confined to disturbed habitats. In addition, each exotic species has different ecological requirements that interact with habitat quality, so that a list of characteristics of habitats and/or traits of species that apply to all situations is not possible.

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