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SPIDER DENSITY AND DIVERSITY IN RELATION TO DISTURBANCE IN AGROECOSYSTEMS IN NEW ZEALAND, WITH A COMPARISON TO ENGLAND

Summary: Spider assemblages were sampled by quantitative sampling in pasture and arable habitats under different management regimes in the lower North Island of New Zealand. Density and species diversity increased with decreasing frequency and/or intensity of disturbance from two species and 1.8 individuals m^{-2} in wheat to 16 species and 130 indiv. m^{-2} in an abandoned, ungrazed pasture. The spider fauna was dominated by introduced species of money spiders (Linyphiidae). The most abundant species, *Lepthyphantes tenuis*, is also the most abundant one in British cultivated habitats. Additional pitfall trap samples from the same location and the Waikato, central North Island, indicated a similar species range containing mainly European species. A sample from a native tussock habitat had a completely different fauna, with only one species shared with the most undisturbed cultivated area. Comparative samples showed that similarly structured, but about twice as species-rich assemblages live in similar cultivated habitats in England.

Keywords: spiders, Lyniphiidae, density, diversity, agroecosystems, disturbance, New Zealand, England.

Introduction

Many spiders are preadapted to habitats with large spatial and temporal variability (Wise, 1993) and constitute an abundant and widespread group of polyphagous predators in ephemeral and disturbed habitats, including cultivated land. In the Northern Hemisphere, spiders are regarded as significant natural enemies of arthropod pests (Riechert and Lockley, 1984; Nyffeler and Benz, 1988; Sunderland *et al*., 1986).

Agricultural habitats in New Zealand are evolutionally recent and bear close resemblance to similar habitats in the Northern Hemisphere, especially Europe, both in terms of flora and fauna (Lövei, 1991). It is likely that spiders play an important role in these habitats. However, information on spiders in agricultural fields in New Zealand is scarce. Martin (1983) listed 47 species collected in pasture during three years near Nelson, South Island. Most of the spiders were not identified to species and general notes on abundance are given for a few species only. European species of linyphiids, *Eperigone fradeorum* (Berland)*, *E. wiltoni* Locket, *Leptyphanthes tenuis* (Blackwall) dominated in pitfall trap catches.

In this paper, we provide the first quantitative data on the density and diversity of spiders in New Zealand cultivated land under different management regimes, and compare the species assemblages with those found in similar habitats in England.

*Misidentified as *Erigone tridentata* (A. MacLachlan, *pers. comm*., Lincoln University, Lincoln, N.Z.)

Methods

Quantitative sampling, New Zealand

Our main study site was on the AgResearch farm at Flock House near Bulls (40°10'S, 175°23'E), in southern North Island, New Zealand. Spiders were collected from nine different agricultural habitats during the southern spring (late November) of 1992. In each habitat, five sampling units of 1 m^2 each were selected and isolated by a 150 mm tall steel ring. Spiders were collected by a modified D-vac suction sampler (30 sec suction) with subsequent hand-searching (Topping and Sunderland, 1994). This method provides a good estimate of 'true' density data for spiders; D-vac samples that are not supplemented by hand-searching underestimate spider density (Topping and Sunderland, 1994).

We selected nine habitats forming a series of management operations (disturbance) of different intensity and frequency:

1. Conventionally managed spring wheat paddock {CW}, in its second consecutive year in wheat.
2. Organically managed spring wheat {OW}, first year in wheat. This plot had an 'organic' certification, conforming to the international Bio-Gro standards. No artificial fertiliser or pesticide was applied. Weeds were controlled mechanically, twice during early spring, when the wheat plants were not taller than 15 cm. The previous crop was a ryegrass (*Lolium perenne* L.) - white clover (*Trifolium repens* L.) pasture.

3-5. Ryegrass - white clover pasture blocks subjected to rotational sheep grazing at high (HG; 28 ewes ha^{-1}), medium (MG; 15 ewes ha^{-1}) and low stocking rates (LG; 5 ewes ha^{-1}). An area within the paddock was grazed for about one week every 15 weeks.

6. a ryegrass - white clover pasture ungrazed for 6 months {NG}, previously under rotational grazing at medium stocking rates by sheep.
7. a ryegrass - white clover pasture abandoned for one year {AP}, previously under rotational grazing at medium stocking rates by sheep. Habitats marked 1-7 were 2 - 2.3 ha in size.
8. a roadside grassy verge, subject to mowing once a year, during the summer {RV}. The dominant plant species were perennial ryegrass, *Poa annua* L., *Phleum pratense* L., and sparse flowering weeds (*Matricaria* sp., *Lamium* sp., A. Maclean and J.M. Hickman, pers. comm.).
9. An experimental plot of species-rich pasture (0.5 ha), planted with a grass/herb mixture containing 16 species {HP}. This plot was planted two years before the sampling, and was not treated, cut or grazed.

Pitfall trapping, New Zealand

Additionally, spiders were collected by pitfall trapping from an organically managed, ungrazed plot of serradella (*Ornithopus sativus* Brotero) at Flock House, over seven weeks between 20 December 1990 and 7 February 1991. The serradella was in its first year, and the plot was free of weeds, except sparse mayweed (*Matricaria* sp.) plants around the edges. Ten pitfall traps were deployed along a straight line, starting from the edge of the paddock and running towards the centre. Individual traps were 10 m from each other. A pitfall trap consisted of a 0.5 L plastic pot filled with 300 mL of 70% ethylene glycol, and covered by a metal square 'roof' to protect the catch from birds, small mammals and rain. Traps were controlled weekly and the catch was collected, sieved, and stored in 70% ethanol until identification. The total trapping effort was 490 trap-days.

Two further series of pitfall trap sampling were used for comparisons, collected from two pastures near Hamilton (37°47'S, 175°17'E), in the Waikato region of the North Island, New Zealand, during October-December 1990. Site A at Ruakura was sown in 1980 with perennial ryegrass and white clover (*Trifolium repens* L.). At the time of sampling, it had substantial ingress of *P. annua* and was grazed by dairy cows. Trapping effort here was 350 trap-days. Site B, Rukuhia, was sown in 1978 with perennial ryegrass cv. 'Grasslands Nui' and white clover cv. 'Grasslands Pitau'. By 1990, it also had ingress of *P. annua*. This pasture was grazed by sheep. The trapping effort was 560 trap-days. At both sites, 10 pitfall traps, with ethylene glycol as preservative, were deployed.

Quantitative sampling from non-cultivated habitat, New Zealand

For comparison with the spider assemblage of cultivated habitats, ten D-Vac suction samples of $1 m^2$ (using the metal ring and hand searching as for the other quantitative samples) were also taken from a scarce tussockland habitat, dominated by *Chinochloa rubra* on the central Volcanic Plateau of the North Island near the top of the Desert Road (850 m a.s.l.; 39°13'S, 175°45'E), in November 1992.

Quantitative sampling, England

Intercontinental comparisons of the assemblage structure were made with spider assemblages collected from two fields of winter wheat in Sussex, southern England (Grid Refs. TQ0403, 50°49'N, 00°31'W, and TQ1807, 50°51'N, 00°19'W, Both fields were sampled using 15 density samples of $0.5 m^2$ each in an identical manner to that used for the New Zealand sampling (Topping and Sunderland, 1994). These were conventionally managed winter wheat fields receiving fungicide and fertiliser but no insecticide applications during the sample seasons (i.e. none were necessary). Both fields were in rotation with grass and oil-seed rape. TQ 1807 was in grass the year before, the other in wheat. The fields were at 20 m and 70 m a.s.l., respectively.

Table 1: *Total spider catch resulting from density sampling of nine agricultural habitats, arranged in decreasing degree of disturbance, at Flock House, Bulls, New Zealand. CW - conventional wheat; OW - organic wheat; HG, MG, LG, NG - grazed paddocks, with high, medium, low and no grazing; RV - roadside verge; AP - abandoned pasture; HP - herb/ pasture. For more details, see Methods.*

Species	CW	OW	HG	MG	LG	NG	RV	AP	HP	Total
LINYPHIIDAE										
Erigone wiltoni	8	0	3	76	24	15	1	2	0	129
Eperigone fradeorum	0	0	4	0	0	0	0	0	0	4
Erigonine Immatures	21	4	0	50	41	1	0	0	1	118
Diplocephalus cristatus	0	0	0	0	0	0	0	2	2	4
Microtenonyx subitaneus (O.-P. Cambridge)	0	0	0	0	0	0	1	0	0	1
Lepthypantes tenuis	3	3	5	2	37	5	40	37	21	153
L. tenuis immatures	1	2	11	11	69	49	403	184	268	998
Diplocenta spp.	0	0	0	0	0	0	0	1	0	1
Mynoglenes diloris	0	0	0	0	0	3	35	4	32	74
M. diloris immatures	0	0	0	0	2	15	98	136	213	464
THERIDIIDAE										
Th1	0	0	0	0	0	0	0	0	1	1
Th2	0	0	0	2	1	2	5	4	1	15
Th2 immature	0	0	0	0	0	0	1	3	30	34
Th3	0	0	0	0	0	0	0	0	1	1
Th4	0	0	0	0	0	0	0	0	1	1
Th5	0	0	0	0	0	0	0	1	0	1
Th5 immature	0	0	0	0	0	0	0	1	0	1
Th7	0	0	0	0	0	0	0	2	5	7
Th7 immature	0	0	0	0	0	0	0	8	3	11
TETRAGNATHIDAE										
Tetragnatha spp.	0	0	0	0	0	0	0	0	2	2
ARANEIDAE										
Ar1 immatures	0	0	0	0	0	0	1	1	1	3
Ar2 immatures	0	0	0	0	0	0	0	2	1	3
SALTICIDAE										
Sa1 immature	0	0	0	0	0	0	0	1	0	1
Sa2	0	0	0	0	0	1	0	0	0	1
LYCOSIDAE										
Ly1	0	0	0	0	0	2	0	4	11	17
Ly11 Immatures	0	0	2	0	1	3	0	85	16	107
OXYOPIDAE										
Ox1	0	0	0	0	0	0	0	2	0	2
Immatures	0	0	0	0	0	0	0	3	1	4
GNAPHOSIDAE										
Anzacia gemmea Dalmas	0	0	0	0	0	2	0	0	0	2
Anzacia spp. immature	0	0	0	0	0	1	0	0	0	1
CLUBIONIDAE										
Clubiona clima Forster	0	0	0	0	0	0	0	1	0	1
Immatures	0	0	0	0	0	0	2	3	0	5
CYATHOLIPIDAE										
Tekelloides spp.	0	0	0	1	0	0	0	0	0	1
Unknown Family										
Un1 immatures	0	0	0	0	0	0	2	2	42	46
Total	33	9	25	142	174	99	599	491	651	2213
Adults	11	3	12	81	62	30	82	60	77	418
Immatures	22	6	13	61	112	69	507	431	574	1795
Number of species	2	2	4	4	5	7	8	16	14	23
Density, individuals m^{-2}	6.6	1.8	5.0	28.4	34.8	19.8	120.0	98.2	130.0	

Pitfall trapping, England

Pitfall trap samples from two perennial ryegrass pastures, obtained from the northeast of England (Grid Ref. NZ 1367, 55°00'N, 01°48'W, 100 m a.s.l.) were compared to pitfall trap catches from New Zealand.

Pitfall traps consisted of 110 mm deep x 85 mm diameter polypropylene cups, with undiluted ethylene glycol as preservative. Lids or covers were not used on the traps. Traps were placed in a transect across the sampled area consisting of 12 traps 1 m apart. The first nine undamaged traps recovered were used in the analysis.

Both pasture sites were 1 y old perennial ryegrass swards. Two cuts of silage were taken during the sample year and the sites were grazed by cattle afterwards. The samples were taken in late May which corresponded in season to those taken in New Zealand. The total trapping effort was 360 trap-days

Evaluation and identification

To describe the diversity of spider assemblages, we used species richness (S), which is the simplest but legitimate measure of diversity, and is often as informative as the more complicated diversity indices (Southwood, 1978).

All spiders were identified using the available identification keys (Forster, 1967, 1970, Forster and Wilton, 1968, 1973; Forster and Blest, 1979; Roberts, 1987, Forster *et al*., 1988). The taxonomic status of many New Zealand spider species is still in doubt, hence a number of morpho-species encountered could not be identified and were allotted code numbers. Nomenclature of the European species follows Roberts (1987).

Results

Spider assemblages in relation to disturbance in New Zealand

A total of 23 species of spiders were identified in the quantitative samples from nine habitats sampled at Flock House. Among habitats, spider species richness ranged between two and 16, and the densities varied between 1.8 and 130 individuals m^{-2} (Table 1).

There was a general trend towards higher numbers of individuals and species as disturbance (defined as the frequency/intensity of agricultural management and/or grazing) decreased. Very high disturbance levels of the two cultivated sites resulted in low spider density and a species-poor assemblage (two species). The most disturbed habitats were the pasture and cultivated ones. These had a simple spider assemblage, comprising the introduced species *L. tenuis*, *E. wiltoni*, *Mynoglenes diloris* (Urquhart) and a few incidentals such as *Eperigone fradeorum* and *Diplocephalus cristatus* (Blackwall) (Tables 1- 3). Only three native species were regularly recorded in the agricultural samples

Table 2: *Spider assemblages on an experimental pasture plot, Bulls, North Island, New Zealand. Each sample consited of 10 pitfall traps.*

	Date							
Species	27 Dec	3 Jan	10 Jan	17 Jan	24 Jan	31 Jan	7 Feb	Total
LINYPHIIDAE								
Erigone wiltoni	5	0	0	0	0	0	0	5
Eperigone fradeorum	0	1	0	0	0	0	1	2
Diplocephalus cristatus	0	0	0	0	0	0	2	2
Ostearius melanopygius (O-P. Cambridge)	1	0	0	0	0	0	0	1
Lepthyphantes tenuis	10	15	3	9	19	20	40	116
Mynoglenes diloris	13	5	10	6	8	6	4	52
LYCOSIDAE								
Ly1	2	2	2	2	0	9	12	29
DOLOMEDIDAE								
Do1	1	0	0	1	0	0	0	2
THERIDIIDAE								
Th2	1	0	0	0	0	1	0	2
Total	33	23	15	18	27	36	59	211

Table 3: *Spider assemblages on pastures in the Waikato region, North Island, New Zealand, according to results of pitfall trap catches.*

Location, species	Date					Total
	25 Oct	15 Nov	22 Nov	29 Nov		
Ruakura						
LINYPHIIDAE						
Erigone wiltoni	0	34	0	19		53
Eperigone fradeorum	2	1	0	6		9
Lepthyphantes tenuis	2	2	5	4		13
Mynoglenes diloris	1	1	2	3		7
LYCOSIDAE						
Ly1	2	5	4	4		15
Total	7	43	11	36		97
Rukuhia	4 Oct	11 Oct	25 Oct	15 Nov	6 Dec	Total
LINYPHIIDAE						
Erigone wiltoni	38	19	4	33	96	190
Eperigone fradeorum	11	8	4	10	26	59
Latesia bellissima	0	0	0	0	1	1
Diplopecta spp.	1	0	0	0	1	2
Lepthyphantes tenuis	5	10	1	12	15	43
Mynoglenes diloris	3	3	0	6	11	23
LYCOSIDAE						
Ly1	1	4	5	8	6	24
Total	59	44	14	69	156	342

(*M. diloris*, Th2 and Ly1). Almost all species recorded from these habitats were money spiders (Linyphiidae).

The organically managed wheat field did not support more spiders than the conventionally managed one: both had only two species, and the density ratio was 3.5:1 in favour of the conventional field (Table 1). For the grazed pastures, the species richness steadily increased with the decreasing intensity of grazing (from high intensity grazing to abandoned pasture). In contrast, the density was highest in the least grazed habitat, and the medium-grazed habitat had higher spider population density than the abandoned one (Table 1). Density but not species richness was three times greater in the roadside verge than the least grazed pasture. Spider density in the other two types of 'abandoned' habitats (AP and HP) was similar to that recorded in the roadside verge habitat. Species richness, however, was higher (Table 1).

In habitats with reduced disturbance, *E. wiltoni* no longer formed a significant part of the assemblage. In contrast, *L. tenuis* numbers were higher. *M. diloris* did not seem to tolerate grazing: of all the grazed habitats, only two immatures (and no adults) were caught in the low-intensity grazed habitat. The prevalence of this species was consistently higher in less disturbed habitats.

The trends in abundance estimates of the adult and immature stages roughly coincided, although habitats with the highest densities had disproportionately high numbers of immatures (Table 1).

Spider fauna sampled by pitfall traps

Flock House, Manawatu

A total of 211 individuals of nine species were collected (Table 2). Weekly catches ranged between two and seven species, and 15- 59 individuals. *L. tenuis* was the most numerous species in pitfall trap samples followed by the native *M. diloris*. These two species made up 80% of the total catch. The third-ranking species was an unidentified native lycosid spider, which was caught, although in small numbers, on all but one sampling occasion.

Ruakura, Waikato

Five species and 97 individuals were caught over the five weeks of pitfall trapping. Four of these were introduced linyphiid spiders. The only native species was the same lycosid caught at Flock House, also constantly present in the captures in small numbers. On two occasions, all the species on the total list were present in the weekly catch. The number of individuals per week ranged between 7 and 56. The catch was dominated by *E. wiltoni* and *L. tenuis* (Table 3).

Rukuhia, Waikato

Seven species and 312 individuals were collected over eight weeks. Five of these were introduced linyphiids, with two natives: *M. diloris* and the unknown lycosid (Table 3). All the species were caught in several weekly or fortnightly catches, and the number of individuals per week varied between 7 and 78. The most numerous species in the catch was *E. wiltoni*, followed by *E. fradeorum, L. tenuis*, and *M. diloris*.

Table 4: *Spiders collected by suction sampling in tussockland habitat on the Volcanic Plateau, North Island. Altitude: 850 m a.s.l. All species thought to be native.*

Species	Number of individuals
LINYPHIIDAE	
Diploplecta communis Millidge	12
Laetesia trispathulata (Urquhart)	4
Laetesia amoena Millidge	1
SYMPHYTOGNATHIDAE	
Sy1	2
THERIDIIDAE	
Th2	14
Th8	1
Th9	1
Th10	1
Th11	1
Th12	1
LYCOSIDAE	
Ly2	1
Total	305
Adults	39
Immatures	266
Number of species	11
Density, individuals m^{-2}	30.5

Spider density in native tussockland

Suction sampling from native New Zealand tussock grassland yielded 305 individuals comprising ten species (Table 4), of which only three were linyphiids. Only the most abundant species (theridiid Th2; see Table 2), was found in samples taken from the least disturbed agricultural habitats (AG, RV, AP and HP).

Intercontinental comparisons

Only partial comparisons were feasible, because of the lack of comparative material. We compared spider density estimates in English and New Zealand wheat fields, and pitfall trap catches in ryegrass pastures in New Zealand and England.

Samples taken using identical methods in Britain showed that wheat fields in England contained more spider species than New Zealand fields (14 and 15 species vs. two species in New Zealand), and densities were five times higher (Table 5). Both faunas were dominated by linyphiid spiders, and *L. tenuis* was abundant in both. The New Zealand assemblage can be considered a subset of the European fauna.

In ryegrass pastures, the same trends were observed as for the density sampling: there were more species and higher numbers in Britain than in New Zealand (Table 6). Linyphiidae again dominated in both areas.

Discussion

Although the structure of the spider assemblages in our study area of agricultural land in New Zealand was similar to that found in England, both species richness and density were lower in New Zealand. The New Zealand samples had approximately half the number of species expected for comparable habitats in England. The majority of the spiders in agricultural habitats in both countries were money spiders (Linyphiidae). Money spiders are highly dispersive (Duffey, 1956; Sunderland, 1991). In contrast, New Zealand native species generally have an allopatric distribution. *M. diloris* appears to be an exception to this and has been observed ballooning in large numbers (R.R. Forster, pers. comm.). Thus, its dispersal ability, atypical of New Zealand native spiders, may explain the high abundance of *M. diloris* in agricultural habitats. *M. diloris* seemed to prefer a complex vegetational architecture, as the highest densities were found in the two habitats which are floristically and structurally the most complex ones (G.L. Lövei and V.K. Brown, unpublished).

Possibly the most interesting aspect of New Zealand agricultural spider assemblages is that the species appear to occupy very similar habitats to those found in Europe. *L. tenuis* is the most abundant spider, with *E. wiltoni*, also common, favouring the shorter, more heavily managed swards. This is almost identical to the situation in Britain where *L. tenuis* is often the most abundant and ubiquitous spider while short swards or arable land

Table 5: *Spider assemblages in two fields of winter wheat in Sussex, England, during spring (May 1990). Samples obtained by D-Vac suction and subsequent hand-searching on 7.5m^2.*

Species	Field A, 17 May	Field B, 21 May
LINYPHIIDAE		
Oedothorax apicatus (Blackwall)	0	2
O. fuscus (Blackwall)	1	1
O. retusus (Westring)	1	6
Tiso vagens (Blackwall)	1	4
Dismodicus bifrons (Blackwall)	4	0
Pananamops sulcifrons (Wider)	2	1
Milleriana inerrans (O.P.-Cambridge)	10	0
Erigone atra	1	3
E. dentipalpis	4	0
E. promiscua	2	5
Meioneta rurestris (C.L. Koch)	5	4
Lepthyphantes tenuis	41	9
Bathyphantes gracilis (Blackwall)	3	1
THERIDIIDAE		
Theridion pallens Blackwall	0	1
TETRAGNATHIDAE		
Pachygnata degeeri Sundevall	1	0
LYCOSIDAE		
Pardosa palustris (L.)	2	3
THOMISIDAE		
Oxyptila sanctuaria (O.P.-Cambridge)	0	1
CLUBIONIDAE		
Clubiona reclusa O.P.-Cambridge	1	0
C. brevipes Blackwall	0	1
Total	283	285
Immatures	204	243
Adults	79	42
Number of species	15	14
Density, individuals m^{-2}	37.7	38.0

are favoured by the *Erigone* species *E. atra* (Blackwall), *E. dentipalpis* (Wider) and *E. promiscua* (O.P.-Cambridge) (Topping, 1991; Topping and Sunderland, 1992). This suggests that the ecological niches occupied by these species are broadly similar between continents. If this is the case, then the lower spider density and diversity in New Zealand agroecosystems could be due to differences in habitat structure and a lower availability of niches, a lack of available colonists or lower prey resource. New Zealand pastures are relatively recent, and were established with European grasses and forage legumes, on land formerly in forest. New Zealand pastures are in appearance similar to those in England. Poor dispersal power may mitigate against successful invasion of this new habitat by endemic species, whilst non-native species may not have had the opportunity to invade. For similar reasons, suitable prey may be low in abundance and thus limit the occupation of the agricultural habitats to only the most efficient competitors. Comparative trophic studies in agroecosystems in Europe and New Zealand would be necessary to give support to either of these hypotheses.

Since most of lowland and mid-altitude areas in New Zealand were covered with forests until the arrival of man (Wardle, 1991), tussockland was chosen as an example of a native habitat most likely to contain spiders pre-adapted to conditions in cultivated habitats. Although our sample was very limited, the structure of the spider community found in tussock was remarkably different from the agricultural samples. All species collected from the tussock grassland site were thought to be endemic to New Zealand and only one (theridiid Th2) was shared with the agricultural sites sampled. Thus, the tussock grassland habitat, although apparently structurally close to some agricultural habitats, seems to be sufficiently different to almost totally exclude species overlap.

This pattern is typical of many other groups of animals and plants in New Zealand (Kuschel, 1990; Lövei, 1991) leading to the peculiar situation whereby the 'imported' agricultural habitats with virtually no evolutionary history in New Zealand are

Table 6: *Adult spider assemblages on two ryegrass pastures from the Tyne Valley, England, obtained by pitfall trapping.*

Species	Field 1	Field 2
LINYPHIIDAE		
Oedothorax fuscus	32	6
Oe. retusus	11	1
Monocephalus fuscipes (Simon)	1	6
Gongylideillum vivum (O.P.-Cambridge)	0	1
Savignya frontata (Blackwall)	0	4
Areoncus humilis (Blackwall)	0	3
Milleriana inerrans	8	3
Erigone dentipalpis	327	98
E. atra	206	143
Meioneta rurestris	3	9
Centromerita bicolor (Blackwall)	0	1
Bathyphantes gracilis	0	7
Lepthyphantes tenuis	6	17
TETRAGNATHIDAE		
Pachygnatha degeeri	1	1
P. clerki Sundevall	2	0
LYCOSIDAE		
Pardosa amentata (Clerck)	1	3
P. palustris	6	0
P. pullata (Clerck)	1	4
CLUBIONIDAE		
Clubiona reclusa	0	0
Total	605	307
Number of species	13	16

found side-by-side with the native habitats. Since agroecosystems are largely species-poor and populated by introduced species, there is great potential for studying the ecological aspects of community organisation in a simplified natural environment. With fewer species, niches may be more easily defined and inter-species interactions may be less complex and more easily investigated.

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