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Geographical distributions, relative abundance and coexistence of *Drosophila aldrichi* and *Drosophila buzzatii* in Australia

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Abstract Climatic data and collection records for the cactophilic *Drosophila aldrichi* and *Drosophila buzzatii* for 97 localities were used to examine the effects of geographical location, season, host plant species and climatic factors on their range and relative abundance. Temporal variation in relative abundance was assessed from monthly collections over 4 years at one locality. Effects of weather variables over the 28 days before each collection were examined. A generalized linear model of the spatial data showed significant geographical variation in relative abundance, and significant climatic effects, with the proportion of *D. aldrichi* higher in the warm season, and increasing as temperature variation decreased and moisture indices increased. The temporal data gave generally concordant results, as *D. aldrichi* proportion was higher in summer and autumn, and increased as maximum and minimum temperatures increased, and as variation in maximum temperature decreased. In a laboratory competition experiment, *D. aldrichi* eliminated *D. buzzatii* at 31°C, but was itself eliminated at 18°C and 25°C. The range of *D. buzzatii* is constrained only by availability of its host plant, *Opuntia* species, although its relative abundance is reduced in the northern part of its distribution. The range of *D. aldrichi*, from central Queensland to northern NSW, Australia, is entirely within that of *D. buzzatii*, and its relative abundance decreases from north to south. Both climate and weather, particularly temperature variability, have direct effects on the relative abundances of the two species, and both likely act indirectly by influencing the outcome of interspecific competition.

Key words: cactophilic *Drosophila*, climate profile, geographical range, interspecific competition, spatial heterogeneity.

INTRODUCTION

The spatial heterogeneity of species abundances may be due to differential effects of environmental factors on the survival and reproduction rates of each species, or to biotic factors – competition, predation or parasitism. Where only two similar species are known to utilize a particular habitat, absence of one or other species from some part of the habitat range may be due to competitive exclusion. But such absence also may be due to other biotic factors or to extremes of some environmental factor(s) that affect the relative abundances of the species in those parts of the habitat range where both species exist. Clearly these effects are not mutually exclusive alternatives (Case & Taper 2000). If the fitness of one species were negatively

correlated with a particular environmental factor, then the relative abundance of that species would be expected to decrease with increasing levels of the environmental factor, to a point where its reduced fitness was such that it could be competitively excluded by the other species. While this is one possibility, the boundaries of a species range may be determined solely by one or more interacting environmental factors, by biotic factors that vary spatially, or by an absence of genetic variation that would allow adaptation and range expansion (Parsons 1991; Hoffmann & Blows 1994; Brown *et al.* 1996; Hoffmann *et al.* 2003). In the simplest case, the species range and boundaries may be determined by the availability of an essential resource, for example, the range of an insect species that is specific to a particular host plant being entirely fixed by the host plant range.

Drosophila aldrichi and *Drosophila buzzatii* in Australia provide a model system for testing the relationship between relative abundance and environmental variables. Both species are members of the *mulleri* subgroup of the *repleta* species group, and both are

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specific to necrotic cladodes (rots) of prickly pear cacti, *Opuntia* spp., as their feeding and breeding habitat. The collection records reported in this article show that they are the only such cactophilic *Drosophila* species utilizing this habitat in Australia. Available evidence indicates that *D. buzzatii* was introduced from Argentina (Barker *et al.* 1985) and *D. aldrichi* from Texas (Krebs & Barker 1993), both about 70 years ago. Thus, they are sympatric only in Australia, and here are utilizing new host plants of the genus *Opuntia*, that is, species that are not present in their endemic regions, with the exception of the use of *Opuntia ficus-indica* by *D. buzzatii*, and possibly *Opuntia stricta* by *D. aldrichi*.

In natural systems, closely related specialist species tend not to be found together (Price 1984), as exemplified by the cactophilic *Drosophila* species of the Sonoran and Mojave deserts in North America. Each of these species is specific to one or a few cactus species, and they rarely overlap host plants (Heed & Mangan 1986; Ruiz & Heed 1988). In contrast, *D. aldrichi* and *D. buzzatii* overlap completely in host plants utilized in localities where both *Drosophila* species are present. Necrotic cladodes returned from these localities usually yield both species (Barker *et al.* 1984), so they are coexisting in the same breeding habitat. Although direct evidence for interspecific competition is not available, intraspecific competition for larval food resources was demonstrated in natural populations of *D. buzzatii* by Robertson (1987). This work was extended by Thomas (1993), who showed that variation in body size of wild *D. buzzatii* adults was determined primarily by variation in the quality of nutrition available to larvae, as these adults were consistently at least 25% smaller than predicted for optimal nutrition. Such intraspecific competition would be predicted also for *D. aldrichi*, although empirical evidence is not available. Interspecific competition therefore could be expected in natural rots, and has been demonstrated in the laboratory (Krebs & Barker 1991), where differences in temperature, host plant species and larval age affected the relative performance (pre-adult survival, development time and body size) of these species (Krebs *et al.* 1992; Krebs & Barker 1993, 1995). Such interspecific competition, as well as environmental and other biotic effects, may be a factor affecting the relative abundances of these species in natural populations.

Species abundances often vary along latitudinal gradients (Ricklefs & Schluter 1993; Rosenzweig 1995). This variation may be due to climatic factors (temperature, rainfall, solar radiation) that are correlated with latitude, or to latitudinal variation in biotic factors (predation, parasitism, interspecific competition). Equally, abundances may vary over other spatial scales (e.g. longitude, elevation) for similar reasons. Attempting to disentangle the effects of these factors

and interactions among them will contribute to a better understanding of community structure and species boundaries. Here we use field collection records of *D. aldrichi* and *D. buzzatii* to evaluate the relative importance of climatic and weather variables, geographical location, interspecific competition and host plant species on their distribution and abundance. We also tested the effect of temperature on the relative abundance of the two species using a simulated natural environment in laboratory population cages.

METHODS

Collections

In the early 1920s, *Opuntia* (prickly pear) cacti were widely distributed over vast areas of eastern Australia (Fig. 1). After the release of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) as a biological control agent in 1925, control of the prickly pears was achieved by 1940, with their distribution reduced to isolated patches (Mann 1970), which mostly still remain with

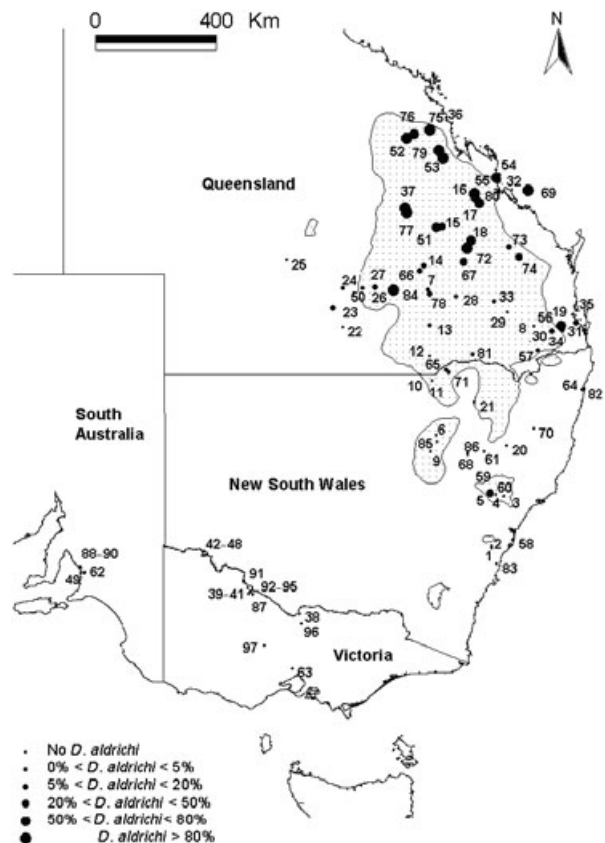


Fig. 1. Collection localities (code numbers), proportion of *Drosophila aldrichi* among collected cactophilic flies at each and distribution of the main *Opuntia* infestations in 1920 (shaded areas).

both host and parasite present. In addition to the main infestation area shown in Fig. 1, isolated patches of *Opuntia* occur in southern NSW, Victoria and South Australia. Since about 1940, suitable habitat for these two *Drosophila* species has been absent, or at least sparse, between *Opuntia* patches that maintain apparently continuous fly populations.

Between December 1971 and March 2002, *Drosophila* collections were made in 97 localities where *Opuntia* cacti occurred (Fig. 1). Most localities were in Queensland and NSW, with some in Victoria and South Australia, and in all, covering the full range of the *Opuntia* species distribution in eastern Australia. In addition to the cactophilic *Drosophila* (*D. aldrichi* and *D. buzzatii*), various other *Drosophila* species were collected. Here we deal only with the two cactophilic species and will refer to the numbers collected of each of them and to total numbers as the sum of the numbers of each in any collection. Most collections were by netting from fermenting banana baits, with some by direct aspiration from rotting cladodes in the field (particularly in winter months when flies are less active), or by returning rots to the laboratory and daily collection of emergences. Wild adults and rotting cladodes were collected at the same time at each of 10 localities (18 collections). For nine collections, the proportions of *D. aldrichi* were higher among wild adults. Overall, proportions of *D. aldrichi* were not significantly different between the two collection methods ($P = 0.19$), that is, no bias due to collection method.

A total of 344 collections gave 130 966 cactophilic flies, with the total number per collection ranging from one (after considerable effort in a winter month) to 9452 emergences from 45 rots collected on 1 day at one locality (mean = 381 ± 770). With one exception, *D. buzzatii* was found wherever there was *Opuntia* cactus, including some localities additional to the 97 used here where its presence was checked, but numbers were not recorded. Neither of the cactophilic species has been found in numerous other collections in localities without *Opuntia* (Bock 1976 – museum records of Australian Drosophilidae, and S. F. McEvey pers. comm. 2004 – 2600 collections throughout Australia). Both species therefore are specific to the cactus niche.

Five *Opuntia* species occurred in the region sampled – *O. stricta* (38 localities), *Opuntia tomentosa* (17), *Opuntia streptacantha* (2), *Opuntia monacantha* (3) and *O. ficus-indica* (23), while 12 had *O. stricta* and *O. tomentosa*, one had *O. stricta* and *O. monacantha* and one had *O. stricta*, *O. tomentosa* and *O. streptacantha*. However, *O. streptacantha* was present only in central Queensland, *O. ficus-indica* only in Victoria and South Australia, *O. tomentosa* primarily in Queensland (one locality in northern NSW) and *O. stricta* throughout the *Opuntia* distribution in Queensland and NSW, and at two localities in Victoria.

At one locality ('Yarrowonga' – locality 5 in Fig. 1), collections were made every month over 4 years (from February 1974 to January 1978, except August and November, 1977). Each month, collections were made at 10 designated sites within an area of about 250 m × 120 m (see Barker *et al.* 1986), and a subjective estimate was made of the amount of 'collecting effort' expended.

Climatic data

For all 97 localities, climatic variables were estimated using the BIOCLIM program of the ANUCLIM 5.1 package (Houlder *et al.* 2000). With the position of a locality described by latitude, longitude and elevation, all 35 climatic variables that can be produced by BIOCLIM were estimated for each locality. Principal component analysis was then applied to these data for each locality (SAS Institute 1985) to provide a summary of the climatic environment for each. A separate principal component analysis was applied to the 35 climatic variables for the 52 localities in the *D. aldrichi* distribution.

Statistical analyses

Two sets of analyses were performed. The first was to determine the effects of geographical location and environmental variables on the proportion of *D. aldrichi*, using the data for the 52 localities within the *D. aldrichi* distribution. These included six in southern Queensland, at or near the southern extent of the range, where no *D. aldrichi* were collected in samples ranging from 63 to 333 flies. Twenty-eight localities had data for both seasons, and 24 for one or other season only. The first four principal components (PCs) of the climatic data for these localities, which accounted for 95% of the variation (Table 1), were included in the analysis. Analysis of the 'Yarrowonga' data (see later) showed significant effects of month or season of collection on the proportion of *D. aldrichi*. Although there are a large number of collections from the 52 localities, results could be biased by any confounding of locality and month of collection, for example, if all or most collections in a given month were only from localities with a high proportion of *D. aldrichi*. Thus, collections at each locality were sorted to two 'seasons': (i) warm (summer-autumn) – collections in December to May; and (ii) cool (winter-spring) – collections in June to November. For locality-season classes with more than one collection, a pooled estimate of *D. aldrichi* proportion (total number of *D. aldrichi*/total number of flies) was used. By pooling the data within season-locality classes, rather than taking the mean proportion over collections, col-

Table 1. Principal components analysis (PC1–PC4) for 35 climatic variables estimated for each of 52 localities in the *Drosophila aldrichi* distribution area.

	PC1	PC2	PC3	PC4
Eigenvalue	18.9	10.7	2.2	1.3
Percentage variation explained	54.1	30.6	6.4	3.6
Eigenvectors				
Annual mean temperature	0.05	0.28	0.12	0.18
Mean diurnal range	-0.21	-0.07	-0.19	0.17
Isothermality	-0.02	-0.03	-0.58	0.29
Temperature seasonality	-0.21	-0.09	0.09	0.04
Max temperature of warmest week	-0.20	0.09	0.11	0.19
Min temperature of coldest week	0.17	0.18	0.15	-0.03
Temperature annual range	-0.22	-0.08	-0.04	0.11
Mean temperature of wettest quarter	-0.11	0.23	0.21	0.15
Mean temperature of driest quarter	0.13	0.23	0.13	0.10
Mean temperature of warmest quarter	-0.10	0.23	0.23	0.21
Mean temperature of coldest quarter	0.14	0.23	0.05	0.09
Annual precipitation	0.23	-0.03	0.02	0.11
Precipitation of wettest week	0.21	0.08	0.01	-0.05
Precipitation of driest week	0.09	-0.09	0.16	0.63
Precipitation seasonality	0.10	0.25	-0.24	-0.03
Precipitation of wettest quarter	0.22	0.06	-0.04	0.02
Precipitation of driest quarter	0.14	-0.23	0.11	0.13
Precipitation of warmest quarter	0.22	0.06	-0.05	-0.01
Precipitation of coldest quarter	0.19	-0.13	0.19	0.17
Annual mean radiation	-0.18	0.19	-0.01	0.07
Highest week radiation	-0.21	0.03	0.24	0.02
Lowest week radiation	0.01	0.28	-0.20	0.11
Radiation seasonality	-0.08	-0.24	0.31	-0.06
Radiation of wettest quarter	-0.22	-0.00	-0.05	-0.12
Radiation of driest quarter	0.08	0.25	0.15	0.09
Radiation of warmest quarter	-0.23	0.01	0.09	0.04
Radiation of coldest quarter	0.01	0.29	-0.14	0.13
Annual mean moisture index (MI)	0.22	-0.07	0.01	0.03
Highest week MI	0.22	0.00	0.01	-0.15
Lowest week MI	0.14	-0.22	0.04	0.21
MI seasonality	0.06	0.22	0.17	-0.30
Mean MI of highest quarter MI	0.22	-0.01	0.05	-0.12
Mean MI of lowest quarter MI	0.15	-0.21	-0.09	0.16
Mean MI of warmest quarter MI	0.22	0.04	-0.13	-0.01
Mean MI of coldest quarter MI	0.18	-0.17	0.14	0.02

Eigenvectors ≥ 0.2 or ≤ -0.2 in bold.

lections with small numbers of flies will have less weight, and noise from monthly fluctuations at a locality will be averaged out to some degree. In addition to season and the PCs of the climatic variables, latitude, longitude, distance from the coast, elevation and cactus species were recorded for each locality. Since the relationships with latitude and longitude were not linear, quadratic and cubic terms were included. Distance from the coast provides a further coordinate to latitude and longitude for geographical location, and was included because climatological zones in eastern Australia tend to run parallel to the coast (Nix 1982). That is, localities on the same longitude but at different latitudes would be in quite different climatological and ecological regions. Four species of cactus (*O. stricta*, *O. tomentosa*, *O. streptacantha* and

O. monacantha) occur in the *D. aldrichi* distribution area, and a numerical code was used to describe the cactus species present at each locality: *O. stricta* – 1, *O. tomentosa* – 2, *O. streptacantha* – 3 and *O. stricta* and *O. tomentosa* or all three species – 4 (the locality with *O. stricta* and *O. monacantha* was coded as *O. stricta* only).

The second analysis assessed effects of variation in weather conditions preceding each of the 46 collections on the proportion of *D. aldrichi* at one locality ('Yarrowonga' – locality 5 in Fig. 1). Collections were classified by season: summer – December to February, autumn – March to May, winter – June to August and spring – September to November (17 season classes over the 4 years). Weather variables (Table 2) for the 28 days preceding each collection were obtained from

Table 2. Weather variables recorded for the 28 days preceding each collection at ‘Yarrowonga’

Variable	Details
MaxT – maximum temperature	Average over 28 days
MinT – minimum temperature	Average over 28 days
RangeT	MaxT–MinT
Xmax	Highest temperature during the 28 days
Xmin	Lowest temperature during the 28 days
Xrange	Xmax–Xmin
Rain	Total precipitation over 28 days
RainDays	Number of days with rainfall
RH	Average relative humidity
MaxSD	Standard deviation of MaxT
MinSD	Standard deviation of MinT
RangeSD	MaxSD–MinSD
RHSD	Standard deviation of RH
MaxCV	Coefficient of variation of MaxT
MinCV	Coefficient of variation of MinT
RangeCV	Coefficient of variation of RangeT
RHCV	Coefficient of variation of RH

the nearest Bureau of Meteorology station (29 km distant from ‘Yarrowonga’) for daily maximum and minimum temperature, rainfall and 1500 h relative humidity. From February 1975 (collection 13) on, extreme maximum and minimum temperatures since the preceding collection were recorded on site; before this, these extreme values were taken from the weather station records. Each month, the incidence of rotting cladodes was recorded using a subjective scale (zero – no or very few rots found, to three), and was included in the analysis as a factor, coded as Rots.

For both analyses, a stepwise procedure was used to suggest which terms may be required in the final model, using the statistical package R (R Development Core Team 2003) and its stepwise procedure, STEP. This procedure uses the Akaike Information Criterion (AIC: Akaike 1974) for adding and deleting terms. We used a variant of this criterion, the Bayesian Information Criterion (BIC: Schwarz 1978), which appeared to give better models as suggested by the significance of terms retained in the model. It was assumed the data had a binomial distribution since they were of the form: $P = (\text{Number observed})/(\text{Total number observed})$. Thus, a generalized linear model (GLM) was used, assuming a binomial error structure and using a logit link function [$\text{logit}(p) = \log(p/(1 - p))$], and weighting each observation by the total number observed. It was evident that the data were overdispersed, so in the stepwise function a scale factor was introduced by first finding an initial model using no scaling factor, then estimating a scaling factor from this model. STEP was used again with the estimated

scaling factor to produce a new model to be fitted allowing for overdispersion. Two diagnostic plots were utilized: a Q–Q (quantile–quantile) plot to assess the distribution assumptions, and a residual plot to check the fit of the model and identify potential outliers.

All tests for individual terms were adjusted for other terms in the model of the same or lower order (type II tests). For hypothesis testing, the Wald test statistic (Fox 2002), which has a chi-square distribution, was used. As used here, type II Wald tests for GLM are actually *differences* of Wald statistics. (Differences between statistics for two models, one containing the term, one without it but both ignoring any higher order interactions contained in the final model.)

Potential distribution prediction

In addition to estimating the climatic variables for each locality, BIOCLIM generated a climatic profile for each species, based on the climatic data for those localities where the species was collected. This profile is a statistical summary of the bioclimatic parameters for each location, and included the minimum and maximum values and the 5, 25, 50, 75 and 95 percentile values for each bioclimatic parameter. This profile thus represents the range of climatic conditions at all recorded locations for the species. BIOCLIM also was used to generate a file of the bioclimatic parameters calculated for each point on a digital elevation model (DEM) of Australia on a 0.5° latitude–longitude grid, based on the 9 second DEM (2002). Predicted distributions for each species then were produced by the BIOMAP program in the ANUCLIM package. For each of the bioclimatic parameters, BIOMAP compares the parameter value for each point on the grid with the statistical distribution of that same parameter in the species profile to see if it falls within one of the statistical spans. The predicted distributions of each species were mapped as core environments (all parameters at the grid point fall in the 5 and 95 percentile range), and as the overall predicted distribution (all parameters at the grid point fall in the minimum to maximum range).

Effect of temperature on relative abundance: laboratory test

The laboratory test of interspecific competition between *D. aldrichi* and *D. buzzatii* at each of three temperatures, 18°C, 25°C (both $\pm 0.5^\circ\text{C}$) and 31°C ($\pm 1.0^\circ\text{C}$), used plastic cages (24 cm \times 24 cm \times 8 cm) that held nine food jars. Each food jar contained 30 g *O. tomentosa* tissue, minced, autoclaved and inoculated with six naturally occurring bacteria species and the yeasts *Pichia cactophila* and *Candida sonorensis*,

48 h before placing in the cages. All cages were initiated with 50 mature pairs of one species (control – two replicate cages at each temperature) or 25 mature pairs of each species (experimental – four replicate cages at each temperature). In each cage, half the flies were added initially with two food jars, and half added with the first additional jar. Because of the different generation intervals at different temperatures, one food jar was added every third day at 31°C, fourth day at 25°C and seventh day at 18°C, with the tenth jar placed in a cage replacing the first jar, the eleventh the second, etc. After the addition of every tenth food jar to a cage (approximately two generations), all adult flies were aspirated, sorted by sex and species under light carbon dioxide anaesthesia, counted and returned to the cage.

RESULTS

The proportion of *D. aldrichi* at each of the 97 localities is summarized in Fig. 1, and details for each locality are available at <http://ansc.une.edu.au/ansc/stfstud/staffindex.html> – link through Barker, Stuart. The distribution of *D. buzzatii* appears to be restricted only by the presence of *Opuntia*, but *D. aldrichi* was collected only from the northern part of the cactus distribution – throughout Queensland and some localities in NSW.

Spatial variation and environmental effects on the relative abundance of *D. aldrichi*

Of the 52 localities in the *D. aldrichi* distribution, 30 were sampled on two or more occasions, for a total of 231 collections, with the number of flies per collection ranging from 5 to 9452 (mean = 468 ± 903). Five localities were sampled 10 or more times – locality 31 (10), locality 61 (14), locality 68 (15), locality 16 (18) and ‘Yarrowonga’ – locality 5 (49).

The proportion of *D. aldrichi* was higher in the warm season for 23 of the 28 localities that had data in both seasons (Fig. 2). The proportion was lower in the warm season for five localities: two in the north where it was very high in both seasons, and three in the south where it was very low in both seasons. The proportion of *D. aldrichi* was higher in northern localities than in southern (Fig. 2). The southernmost locality (‘Yarrowonga’) had a higher proportion of *D. aldrichi* in both seasons than other southern localities, except for two (Nos 19 and 78) with very high proportions in the warm season. However, there was only one warm season collection for each, with 43 and 322 flies, respectively, and the apparently aberrant high proportions may have been due to weather conditions or other factors prior to the collection. The correlation coefficient between warm and cool season

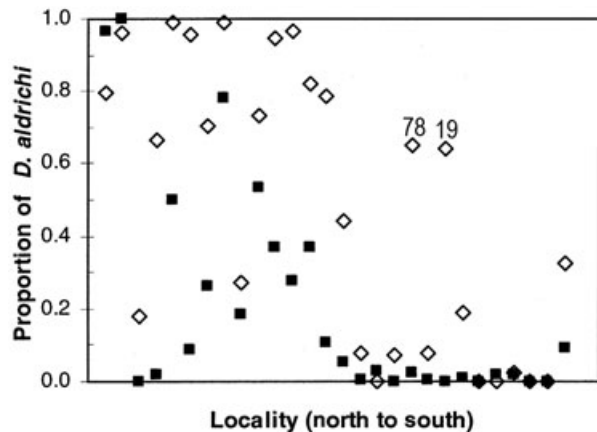


Fig. 2. Mean proportion of *Drosophila aldrichi* at 28 localities where collection data were available for both warm (◇ December–May) and cool (■ June–November) seasons. Numbers on two warm season collections are locality code numbers (see text).

Table 3. Analysis of effects of location, season and climatic variables on the proportion of *Drosophila aldrichi* at 52 localities throughout its distribution

Variable	d.f.	Wald χ^2	P
Latitude – linear (L1)	1	51.329	<<0.001
Latitude – quadratic (L2)	1	3.478	NS
Latitude – cubic (L3)	1	17.921	<0.001
Season	1	73.285	<<0.001
Dcoast	1	18.818	<0.001
Elevation	1	10.379	<0.01
PC1	1	15.697	<0.001
L1 × Elevation	1	10.431	<0.01
L2 × Elevation	1	4.176	<0.05

NS, not significant.

proportions was 0.67 ($P < 0.01$), indicating that the relative magnitude of *D. aldrichi* proportions in the two seasons was generally consistent over localities.

The results of the GLM analysis (Table 3) show, as expected, a highly significant effect for season (compare Fig. 2), with latitude, distance from the coast and PC1 also highly significant. The diagnostic plots indicated the assumptions and fit of the model to be satisfactory, although there are four possible outliers (standardized residual outside the range ±2). The four predicted estimates that were outliers were all for the warm season, with two positive and two negative residuals. None involved small sample sizes, and we have no obvious explanation for these. In addition, a variogram of the residuals shows little evidence of spatial correlation and no further attempt was made to allow for this in the model.

The latitudinal cline in the proportion of *D. aldrichi* is paralleled to some extent by the cactus species

distributions: *Opuntia streptocantha* in central Queensland, *O. tomentosa* from central Queensland to northern NSW, and *O. stricta* increasing in abundance from north to south, so that *Opuntia* species, combined with climatic effects could contribute to the *D. aldrichi* cline. However, at one collection at locality 16, flies collected in the immediate vicinity of each of the three *Opuntia* species were censused separately, and the proportions of *D. aldrichi* were 0.513, 0.551 and 0.674 from *O. stricta*, *O. tomentosa* and *O. streptocantha*, while at another collection at the same site, the proportions of *D. aldrichi* in emergences from *O. stricta* and *O. streptocantha* rots were 0.99 and 0.96, respectively. At locality 50, the proportion of *D. aldrichi* among emergences from *O. stricta* and *O. tomentosa* rots were 0.189 and zero, respectively. Furthermore, the proportion of *D. aldrichi* was very high in some northern localities where there was only *O. stricta* (e.g. locality 55). As compared with its performance on other *Opuntia* species, *D. aldrichi* is not at a competitive disadvantage when utilizing *O. stricta* in the northern (warmer) parts of its distribution.

In the principal component analysis of the 35 bioclimatic variables for all 97 localities, the first two components accounted for 43.0% and 31.8% of the variation, and described similar patterns to those for the 52 *D. aldrichi* localities (Table 1). The first PC describes a gradient of increasing precipitation and moisture indices and decreasing temperature variability and radiation. The second component describes a gradient of increasing temperature, precipitation and moisture index seasonality, and decreasing moisture indices in the lowest week and quarter, precipitation in the driest quarter and radiation seasonality. The plot

of the first two components (Fig. 3) shows general discrimination between localities where *D. aldrichi* was found (together with *D. buzzatii*) and localities with *D. buzzatii* only. The lines drawn in Fig. 3 were fitted by eye to distinguish three zones – both species expected to be present, *D. aldrichi* sometimes present but generally at very low proportion, and *D. buzzatii* only present. Nine localities which might have been expected to have *D. aldrichi* present (based on the PC plot) are marked in Fig. 3. The two labelled ‘S’ were each from collections in August and/or November with very small numbers collected (2, 8 and 28), while the seven points labelled ‘B’ were all single collections per locality (mean number collected = 112) in August or November, that is, collections in months where the seasonal data indicate expected low *D. aldrichi* frequencies. Apart from ‘Yarrowonga’ (Y), three other localities (labelled A) with *D. aldrichi* present are outliers. At these localities, the occurrence of *D. aldrichi* was sporadic and at very low numbers: locality 68 – three *D. aldrichi* in a total of 1745 flies at one of 15 collections, locality 61 – three in a total of 10 159 flies at one of 14 collections, and locality 82 – one in 170 flies at one collection.

Seasonal variation

For the ‘Yarrowonga’ data, the total number of flies collected per month ranged from 12 to 2745 (mean = 130 ± 328). The proportion of *D. aldrichi* varied markedly during the 4-year period (Fig. 4a), with means (over months) in each of the 4 years of 0.281, 0.320, 0.068 and 0.151. The relative numbers

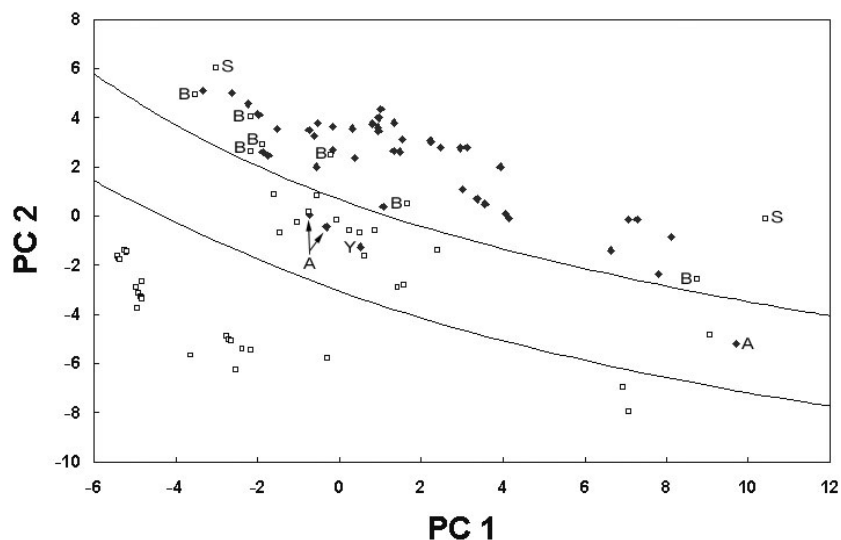


Fig. 3. Plot of the first two principal components (PCs) of 35 bioclimatic variables for all 97 localities where cactophilic flies were collected. (□) *Drosophila buzzatii* only, (◆) both *Drosophila aldrichi* and *D. buzzatii*. Letter codes for some locality points are explained in the text.

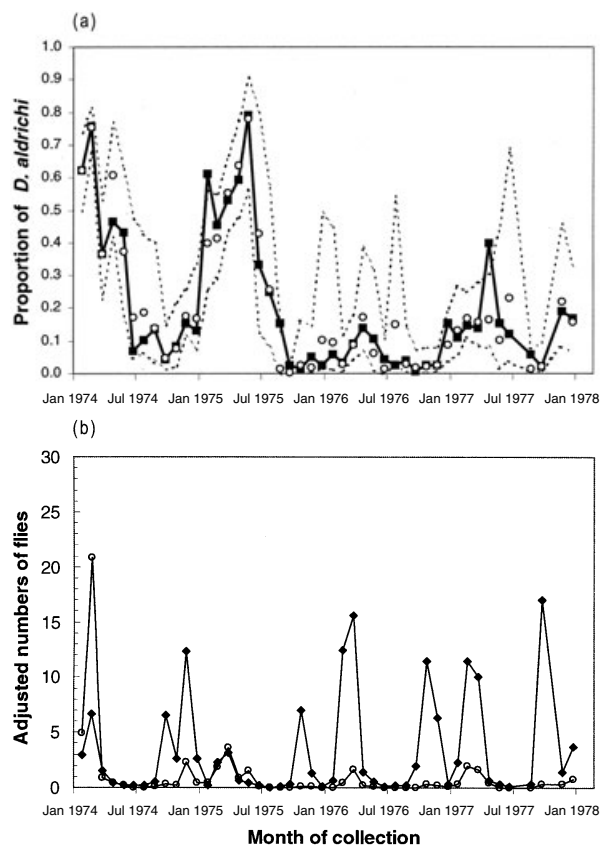


Fig. 4. (a) Observed and predicted proportion of *Drosophila aldrichi* at 'Yarrowonga' in each month over a 4-year period (■ observed proportion, ○ predicted proportion, dotted lines – 95% confidence limits), (b) relative numbers of *D. aldrichi* (○) and *Drosophila buzzatii* (◆) collected at 'Yarrowonga'. February 1974 data are actual numbers collected; all other data are adjusted for estimated collection effort relative to that in February, 1974.

of flies of each species in each collection were standardized by using the actual numbers in the first collection, and adjusting all other collections by the estimated collection effort relative to that of the first collection. These data (Fig. 4b) show that *D. buzzatii* peaked in population size twice a year, primarily in March–April and October–November, while *D. aldrichi* peaked once in March–April. However, the variability among collections in numbers of flies was much greater for *D. buzzatii*, so that *D. aldrichi* proportions (average over the 4 years) were highest in May and June (0.399 and 0.371, respectively), and lowest in October and November (0.025 and 0.042, respectively).

The GLM analysis of the 'Yarrowonga' data indicated a combination of variables that were important in predicting the proportion of *D. aldrichi*, with season, rot effects, and a number of weather variables significant (Table 4). The diagnostic plots indicated that the assumptions for the model did not appear to

Table 4. Analysis of effects of season, rot incidence and weather variables on the proportion of *Drosophila aldrichi* at 'Yarrowonga'

Variable	d.f.	Wald χ^2	P
Season	16	153.585	<<0.001
Rots	3	16.143	<0.01
MaxT	1	10.493	<0.01
MinT	1	13.653	<0.001
RainDays	1	13.767	<0.001
MaxCV	1	22.899	<0.001

MaxCV, maximum coefficient of variation; MaxT, maximum temperature; MinT, minimum temperature.

be violated and the fit was satisfactory, although two possible outliers were identified (standardized residuals > 2.0). These 2 months were February 1975 and May 1977, with the observed proportion of *D. aldrichi* higher than predicted (Fig. 4a). Season effects are clear (Fig. 4a), and overall proportions of *D. aldrichi* for each rot incidence category were: 0 = 0.098, 1 = 0.313, 2 = 0.217 and 3 = 0.038. After adjusting for other variables (type II effects), four weather variables were significant, with the proportion of *D. aldrichi* increasing with MaxT and MinT, and decreasing with MaxCV and RainDays.

Potential distribution prediction

The predicted distributions of both species (Fig. 5) show clearly that the *D. aldrichi* range is entirely within that for *D. buzzatii*. The predicted distribution boundaries of the two species are similar in the north, while that for *D. buzzatii* extends further west. To the south in eastern Australia, the range for *D. aldrichi* is substantially more restricted than that for *D. buzzatii*. The predicted distribution of *D. buzzatii* extends into south-western Australia, where *Opuntia* cacti are known to occur, but no *Drosophila* collections have been made there in localities where cactus is present.

Effect of temperature on relative abundance: laboratory test

Temperature affected the proportions of *D. aldrichi* and *D. buzzatii* on simulated necrotic *O. tomentosa* in population cages (Table 5). *Drosophila aldrichi* maintained a continuous population in control cages at 18°C and 25°C, although the numbers decreased with time at 18°C. However, with *D. buzzatii* present, there were relatively few *D. aldrichi* at the first count, and they were essentially eliminated from all cages by the second count at both 18°C (day 140) and 25°C (day 80), that is, about four generations. In contrast at

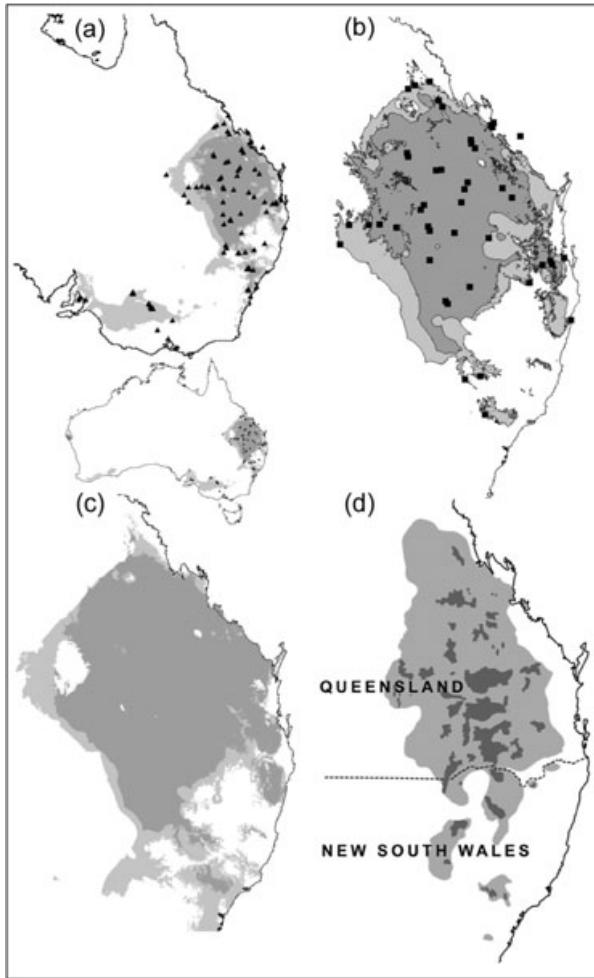


Fig. 5. Maps showing collection locations and predicted potential distributions for *Drosophila buzzatii* and *Drosophila aldrichi* (a). *Drosophila buzzatii* – ▲ collection localities, darker shading = core environment, lighter shading = overall predicted distribution (note area predicted in south-west Australia on small map) (b). *Drosophila aldrichi* – ■ Collection localities, shading as for (a) and (c). Overall predicted distribution for *D. aldrichi* (darker shading) overlaid on that for *D. buzzatii* (lighter shading), (d) distribution of the prickly pear infestation in eastern Australia in 1920, darker shading indicates very dense infestation.

31°C, *D. buzzatii* was eliminated from the cages by the fourth count (120 days, or about eight generations). *Drosophila buzzatii* died out in one control cage at 31°C due to a mould infection.

DISCUSSION

The relative abundances of *D. aldrichi* and *D. buzzatii* are not constant throughout the *Opuntia* cactus distribution in eastern Australia. *Drosophila buzzatii* was collected at all but one of 97 localities (locality 52 – 16 *D. aldrichi*). Although apparently constrained only

by the availability of its host plant, the relative abundance of *D. buzzatii* is reduced in the northern end of its range (Fig. 1). The range of *D. aldrichi* on the other hand is much more restricted, being entirely within that of *D. buzzatii* (Fig. 5c), and its relative abundance decreased from central Queensland southwards (Fig. 1). The questions then are whether the environment in the south is more suited to *D. buzzatii*, less suited to *D. aldrichi*, or both, and whether interspecific competition effects are involved.

Estimated population sizes of the two species at each collection would be invaluable, but our data do not, unfortunately, provide even indirect estimates, as collection effort varied greatly. However, genetic data (microsatellite variation – V. Loeschcke & J. S. F. Barker unpubl., and allozyme variation – J. S. F. Barker unpubl.) indicate that the effective population sizes for *D. buzzatii* at localities in southern NSW and Victoria are lower than further north, suggesting decreased environmental suitability in these southern localities.

In a laboratory experiment with three *Drosophila* species and using a multiple cage system, Davis *et al.* (1998) showed that species range and abundance can be strongly influenced by species dispersal and species interactions. Apparently similar effects in the cactophilic *Drosophila* populations suggest that the environmental suitability for *D. aldrichi* decreases in the southern part of its distribution. A number of localities in northern NSW and southern Queensland are outside the core climatic environment for *D. aldrichi*, and at the margin of the overall predicted distribution as modelled by BIOMAP (Fig. 5b). At three of these localities in NSW (Nos 61, 82, 86 – Figs 1,3 – localities labelled A) the occurrence of *D. aldrichi* was sporadic and at very low numbers. For ‘Yarrowonga’ (No. 5), *D. aldrichi* was not found in 145 flies collected in April 1972. Yet as noted earlier, it had reached a high proportion at the next collection (February 1974), and was present in every one of 46 collections over the next 4 years. However, the proportion of *D. aldrichi* decreased over this time, and at later collections (April 1982: 2237 flies, and April 1983: 142 flies) had decreased further to 0.032 and 0.028, respectively. Even though *D. aldrichi* persisted for some years at ‘Yarrowonga’, collections from three nearby localities (Nos 4, 59, 60: 8.2–17.2 km distant) strengthen the conclusion that these central-northern NSW localities are less favourable for *D. aldrichi*. At these localities, no *D. aldrichi* were collected in 24 collections (8361 *D. buzzatii*) over a 14-year period (1973–86) that spanned the ‘Yarrowonga’ collections (1974–83). Locality 31, in south-east Queensland, also outside the core environment for *D. aldrichi*, provides further evidence that these southern Queensland/northern NSW localities are marginal. Three collections there in 1973–74 (333 *D. buzzatii*) yielded no *D. aldrichi*. At

Table 5. Mean proportions of *Drosophila aldrichi* and mean total number of flies in experimental cages, and mean number of each species in control cages at three temperatures

	18°C – counts			25°C – counts			31°C – counts			
	1	2	3	1	2	3	1	2	3	4
Experimental										
Proportion <i>Drosophila aldrichi</i>	0.07 (0.04)	0 NA	0 NA	0.13 (0.02)	0.01 (0.005)	0 NA	0.63 (0.07)	0.79 (0.13)	0.99 (0.005)	1.00 NA
Total no. flies	294 (56)	240 (16)	308 (26)	291 (29)	258 (46)	299 (26)	102 (21)	124 (36)	160 (28)	192 (13)
Control										
<i>Drosophila aldrichi</i>	425 (86)	191 (30)	77 (28)	146 (2)	183 (36)	360 (3)	94 (50)	105 (26)	135 (6)	184 (34)
<i>Drosophila buzzatii</i>	151 (71)	144 (16)	240 (54)	260 (41)	195 (42)	287 (4)	258 –	185 –	245 –	165 –

Standard errors of means in parentheses. NA, not applicable; –, only one replicate cage.

three collections during 1977–79, *D. aldrichi* was found at low frequencies (0.032, 0.082, 0.049), but was not seen in four later collections during 1982–85 (2157 *D. buzzatii*). The numbers of flies collected and relative abundance of *D. aldrichi* indicate that these localities are most likely subject to ephemeral colonization by this species. The failure of *D. aldrichi* to persist in these southern localities is likely an example of an ‘Allee threshold’, an inability to persist below a critical population density (Keitt *et al.* 2001).

In localities where both species occur, coexistence is not due to intraspecific aggregation in different breeding sites, as found, for example, by Wertheim *et al.* (2000) in a mycophagous insect community. During the period of our collections, 181 rots were collected at random from localities where both *Drosophila* species were found. Adults of both species emerged from 147 (81.2%). Cool season collections are not comparable across *Opuntia* species, as all collected *O. stricta* rots in this season were from south Queensland localities. However, for rots collected in the warm season from northern localities, all of 40 *O. tomentosa* and 11 *O. streptocantha* rots produced both species, as did 76% of 25 *O. stricta* rots (remainder *D. buzzatii* only). Thus, most rots in the region of overlap of the two species are being used by both species.

The result for *O. stricta* might indicate that *D. aldrichi* is at a competitive disadvantage in this species, as compared with *D. buzzatii*. Laboratory experiments show, however, that any such effect is temperature dependent. When raised on *O. stricta* at 25°C, pre-adult viability and body size of *D. aldrichi* were significantly less than for *D. buzzatii* in mixed species cultures (Krebs *et al.* 1992), but at the higher temperature of 31°C, Krebs and Barker (1993) showed *D. aldrichi* to be superior for pre-adult viability and developmental time. Finally, as the species of

Opuntia was not a significant factor in the GLM analysis, the different species apparently have little or no effect on the relative abundance of *D. aldrichi*.

Laboratory experiments (Barker *et al.* 1988) found no evidence for resource partitioning within rots, so that interspecific competition may well influence the relative abundance of the two species. This is supported by the population cage experiment, where *D. aldrichi* was superior to *D. buzzatii* at 31°C, but inferior at 18°C or 25°C. Thus, the seasonal change in proportions of the species in natural populations and the cline in proportion of *D. aldrichi* are likely due both to better performance of *D. aldrichi* at higher temperatures, and to better performance of *D. buzzatii* at lower temperatures.

The GLM analysis of the spatial data showed significant effects for latitude and season, with *D. aldrichi* proportions decreasing from north to south and higher in the warm season (Fig. 2). Distance from the coast and elevation also were significant, with proportion of *D. aldrichi* decreasing with increasing distance from the coast and increasing with elevation. However, after adjusting for geographical location (latitude and Dcoast), the PC1 (climate) effect was highly significant. This effect can be described in terms of two components. All but one locality (No. 84) with PC1 < –2.0 had very low *D. aldrichi* frequencies (generally < 0.1) and these were south-west of a line through localities 14 and 28 (Fig. 1), that is, inland localities with lower rainfall and higher temperature seasonality. For localities where PC1 > –2.0, *D. aldrichi* proportion shows no trend with PC1 (slope = –0.025 ± 0.017, NS), but any association is confounded by north-south and coastal-inland patterns. For example, the seven localities with highest PC1 values are all coastal: the four northern (Nos 32, 54, 55, 69) have an average *D. aldrichi* proportion of 0.448, and the three southern (Nos 31, 35, 82) an

average of 0.023. In general, PC1 effects indicate increasing *D. aldrichi* proportion as temperature variation (diurnal range, annual range and temperature seasonality) decreases, and rainfall and moisture indices increase. As the latter indices increase, rots persist for longer, thus favouring *D. aldrichi*, which is more successful in utilizing older rots (Barker *et al.* 1984).

As latitude and distance from the coast are significant factors after controlling for climate (PC1), geographical variation in factors other than those considered here must be affecting the relative abundances of the two species. For example, complex associations among the *Drosophila* community, the microflora community and physical and chemical attributes of the rots (Barker *et al.* 1984) may vary geographically, and at least partly independent of climatic variation. Similarly, while seasonal effects are certainly temperature dependent, variation among seasons in the yeast species community (Barker *et al.* 1983) could contribute further interacting or independent effects. Among other biotic factors for which no data are available, predators and parasites may exert an influence, as found for parasitoid wasps and *Drosophila melanogaster* and *Drosophila simulans* in southern France (Fleury *et al.* 2004).

Analysis of the 'Yarrowonga' data for the effects of weather variables over the 28 days preceding each collection gave results generally concordant with the spatial analysis. The proportion of *D. aldrichi* was higher in summer/autumn ('warm' season for the spatial data), and after adjusting for seasonal effects, it increased as mean maximum and minimum temperatures increased, and as the coefficient of variation of maximum temperature and number of days with rainfall decreased. The effect of the coefficient of variation of maximum temperature (Table 4) agrees well with the effects of temperature variability in the spatial analysis. As compared with the spatial analysis, where the proportion of *D. aldrichi* increased with increasing rainfall and moisture indices, the negative effect of number of days with rainfall appears anomalous.

Although host plant availability determines the range of *D. buzzatii*, its abundance relative to *D. aldrichi* is reduced in the northern part of its distribution, most likely due to the interacting effects of temperature and lower competitive ability. Effective population sizes are likely reduced in the southern part where *D. aldrichi* is not found. Both climatic (long-term) and weather (short-term) variables, with both influencing the outcome of interspecific competition, affect the range and abundance of *D. aldrichi*.

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