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A collection of Australian *Drosophila* datasets on climate adaptation and species distributions

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The Australian *Drosophila* Ecology and Evolution Resource (ADEER) collates Australian datasets on drosophilid flies, which are aimed at investigating questions around climate adaptation, species distribution limits and population genetics. Australian drosophilid species are diverse in climatic tolerance, geographic distribution and behaviour. Many species are restricted to the tropics, a few are temperate specialists, and some have broad distributions across climatic regions. Whereas some species show adaptability to climate changes through genetic and plastic changes, other species have limited adaptive capacity. This knowledge has been used to identify traits and genetic polymorphisms involved in climate change adaptation and build predictive models of responses to climate change. ADEER brings together 103 datasets from 39 studies published between 1982–2013 in a single online resource. All datasets can be downloaded freely in full, along with maps and other visualisations. These historical datasets are preserved for future studies, which will be especially useful for assessing climate-related changes over time.

Design Type(s)	observation design • time series design • data integration objective
Measurement Type(s)	phenotype • Geographic Distribution
Technology Type(s)	data item extraction from journal article
Factor Type(s)	comparative phenotypic assessment
Sample Characteristic(s)	<i>Drosophila melanogaster</i> • Eastern Australia • <i>Drosophila birchii</i> • <i>Drosophila serrata</i> • <i>Drosophila simulans</i> • <i>Drosophila aldrichi</i> • <i>Drosophila buzzatii</i> • <i>Scaptodrosophila acinata</i> • <i>Scaptodrosophila hibisci</i> • <i>Drosophila bunnanda</i> • <i>Drosophila kikkawai</i> • <i>Drosophila jambulina</i>

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Background & Summary

The Australian *Drosophila* Ecology and Evolution Resource (ADEER) contains three main *Drosophila* data collections: (1) clinal data, (2) species distribution data and (3) genomics data. The clinal and species distribution collections are described in this data descriptor, whereas the genomics data will be described elsewhere. The majority of data was generated by Ary Hoffmann's research group at the University of Melbourne, with contributions from several other Australian researchers (see Acknowledgements).

Drosophila species have long been used as model organisms to answer fundamental questions in biology, and the most intensively studied *Drosophila* species (in particular *Drosophila melanogaster*) are Northern Hemisphere in origin¹. Drosophilids as a broader taxonomic group are very diverse in Australia, with over 300 species identified in the tropical and temperate forests located on the east coast. Australia contains a disproportionately large number of species in the genus *Scaptodrosophila*, many of them endemic to this continent². The ADEER collection broadens the scope of worldwide drosophilid data, by focussing on clinal patterns in traits and genes in Australian drosophilids as well as on thoroughly-studied species distributions. This collection contains data on the ecology and evolution of eleven species in the genera *Drosophila* and *Scaptodrosophila* including rainforest specialists (e.g. *D. birchii*), endemic species (e.g. *D. bunnanda*) and cosmopolitan species (e.g. *D. melanogaster*).

The east coast of Australia spans a gradient of climatic conditions from cool-temperate Tasmania to tropical northern Queensland. This gradient is unique as it occurs within a narrow elevation range and on a small continent with an ancient geology and a rich biodiversity with a high proportion of endemic species across several biomes³. The gradient provides a model system for studying equivalent climatic gradients on other continents, and represents an outstanding natural laboratory for the study of traits and genes that are associated with climatic adaptation⁴. Changes in traits and genes along this gradient (i.e. clines) can arise by natural selection, producing continuous patterns over geographic space. The eastern Australian gradient has been used to investigate the involvement of numerous phenotypic traits and genetic markers in climate adaptation⁴. The clinal data collection contains data from eight species from studies published between 1982–2013 and includes morphological, life-history, stress resistance traits as well as genetic markers. Most of these studies used common garden experiments to test for clinal variation, but some studies were performed in the field.

The species distribution collection includes five species from the *melanogaster* species group (*montium* subgroup) and two species from the *repleta* species group within the genus *Drosophila*, as well as two *Scaptodrosophila* species. These datasets contain presence records from field collections between 1924 and 2013 which are based on previously-published records in the literature, collections made by the dataset authors, and specimens in the Australian Museum^{5–7}. Many species are restricted to the tropics, a few are temperate specialists, and some are broadly distributed across climatic regions. The varied distributions of drosophilid species along the temperate–tropical cline provide a powerful tool for studying climate adaptation and species distribution limits.

Previous work on *Drosophila* species using the Australian cline has demonstrated that monitoring biological changes along geographic climate gradients is a powerful approach for detecting evolutionary shifts under climate change^{8,9}. Ongoing data collections from the eastern Australia cline provide an opportunity to monitor phenotypic traits and genetic markers by comparison to historical data, as climate change proceeds. Such temporal studies are particularly useful for tracking continuing evolutionary responses to climate change as well as dynamically projecting species distributions under ongoing climate change scenarios.

Methods

Clinal data collection

The clinal data collection contains data on morphological, life-history and stress resistance traits, as well as genetic marker data (Tables 1 and 2 (available online only), Fig. 1). All datasets of this kind involve flies collected at multiple locations within their geographic distribution, usually along a north-south gradient on the east coast of Australia. Material and methods for each dataset appear in detail in the original publication; here we provide a general summary of the approaches used.

This clinal data collection includes data recorded at the level of the individual fly (46 datasets), the subgroup level (12 datasets) or the population level (41 datasets). The term population is here used for a group of flies collected at a single geographic location. Distinct collection sites were typically at least 40 km apart. Individual data include morphological, life-history, stress resistance traits and individual genotype at genetic marker loci. Many data were recorded as population frequencies, such as *Wolbachia* infection rate and genetic marker frequency (Table 1 (available online only) and Tables 2 (available online only) and 3). For other datasets the data are available as population means, including morphological, life-history and stress resistance traits and genetic markers. A few datasets report results at the subgroup level. These datasets include traits that were measured per vial (e.g. development time, longevity and mortality), per cage (e.g. mortality and fecundity) or per group of flies (desiccation and starvation resistance, gene expression). In addition, one dataset reports data on isofemale lines¹⁰. Isofemale lines are fly lines that were founded from the offspring of one single wild female (Figs 1 and 2).

Datasets	Species	Publication	Collection years
201 Barker ⁵ <i>S. acinata</i> collection records	<i>S. acinata</i>	Barker ⁵	1995
202 Barker ⁵ <i>S. hibisci</i> collection records	<i>S. hibisci</i>	Barker ⁵	1998
203 Barker <i>et al.</i> ⁶ <i>D. buzzatii</i> and <i>aldrichi</i> collection records	<i>D. buzzatii</i>	Barker <i>et al.</i> ⁶	1971–2002
203 Barker <i>et al.</i> ⁶ <i>D. buzzatii</i> and <i>aldrichi</i> collection records	<i>D. aldrichi</i>	Barker <i>et al.</i> ⁶	1971–2002
204 Schiffer & McEvey ⁷ <i>Montium</i> collection records	<i>D. bunnanda</i>	Schiffer & McEvey ⁷	1924–2005
204 Schiffer & McEvey ⁷ <i>Montium</i> collection records	<i>D. serrata</i>	Schiffer & McEvey ⁷	1924–2005
204 Schiffer & McEvey ⁷ <i>Montium</i> collection records	<i>D. birchii</i>	Schiffer & McEvey ⁷	1924–2005
204 Schiffer & McEvey ⁷ <i>Montium</i> collection records	<i>D. kikkawai</i>	Schiffer & McEvey ⁷	1924–2005
204 Schiffer & McEvey ⁷ <i>Montium</i> collection records	<i>D. sp. cf. jambulina</i>	Schiffer & McEvey ⁷	1924–2005

Table 3. Species distribution datasets for nine drosophilid species. The publication associated with the dataset and collection years are reported.

Fly populations compared for clinal variation in quantitative traits have almost always been maintained in the laboratory prior to testing, for periods ranging from just one generation to several years. The effect of laboratory culture on clinal patterns was specifically investigated in two of the datasets included in this collection using *D. melanogaster*^{11,12}. Almost all clinal studies on quantitative traits in this collection involve a common garden design, where populations are reared in a common environment before they are tested for a specific trait. Flies are therefore kept under controlled temperature and day length and on standard fly medium within a study, but these conditions can vary substantially among studies. A few studies did not use common garden experiments. These include the two studies mentioned above^{11,12} where field flies were preserved in alcohol to measure wing traits. Other exceptions^{13,14} involved clinal variation in fecundity and mortality scored directly under field conditions.

Morphological traits

27 datasets from 15 publications in this collection investigated morphological traits in *D. melanogaster*, *D. serrata*, *D. aldrichi*, *D. buzzatii*, *D. simulans*, or *D. birchii*. The morphological traits include size (10 datasets), wing morphology (20 datasets), pigmentation (2 datasets) and lipid content (1 dataset).

Thorax length, measured from the anterior margin of the thorax to the posterior tip of the scutellum, is most often used as a measure of size and was investigated in four *D. melanogaster* studies^{10,15–17} in *D. aldrichi* and *D. buzzatii*¹⁸ and in *D. simulans*¹⁶. **Mass** was used as a measure of size in one *D. serrata* study¹⁹. In addition, **egg size** was measured in one *D. melanogaster* study²⁰.

Wing morphology was investigated in seven *D. melanogaster* studies^{11,12,15–17,21,22}, in *D. aldrichi* and *D. buzzatii*¹⁸, in *D. birchii*²³, in *D. serrata*^{19,24} and in *D. simulans*¹⁶. Wings were removed from individual flies and mounted on slides, and wing traits were either directly measured under a microscope^{11,12,17,22} or measured from landmarked images captured under the microscope^{15,16,18,19,21}.

Pigmentation was investigated in one *D. melanogaster* study and was scored by visual examination using four phenotypic classes²⁵.

Lipid levels were scored in one *D. melanogaster* study where adult females were initially dried in an oven for 48 h and then soaked in ether for 24 h to extract the lipids⁹.

Life-history traits

There are 24 datasets in this collection from 13 publications that investigated life-history traits in *D. melanogaster*, *D. serrata*, *D. aldrichi*, *D. buzzatii*, *D. simulans*, or *D. birchii*. This includes traits related to development (11 datasets), mortality (8 datasets) and reproduction (8 datasets).

Egg-to-adult development time was investigated in two *D. melanogaster* studies^{21,26}, *D. aldrichi* and *D. buzzatii*¹⁸, *D. birchii*²³, *D. serrata*²⁷ and in *D. simulans*²⁸. Development time was measured from the midpoint of the egg laying period to adult eclosion (emergence from the pupal case). In addition, egg development stage was examined in female *D. melanogaster* after being exposed to diapause-inducing conditions for 28 days²⁹.

Mortality was investigated in *D. melanogaster*^{13,14,30}, *D. aldrichi* and *D. buzzatii*¹⁸ and *D. serrata*²⁷. In *D. melanogaster*, mortality was recorded in field cages held at temperate winter conditions near Melbourne¹³ and at tropical winter conditions in Cairns¹⁴. In addition, **longevity** of once-mated females was scored under standard laboratory conditions³⁰. The flies were transferred to fresh vials every day, and at each transfer, all vials were examined for dead flies³⁰. In *D. aldrichi* and *D. buzzatii*, larvae to adult **viability** was scored after rearing the flies at three temperatures treatments¹⁸. **Egg to adult** and **pupal to adult viability** were scored in *D. serrata* collected before and after winter²⁷. To score egg to adult and pupae to adult viability, vials were scored until no new adults emerged and the number of pupae in each vial was counted to obtain pupal viability data²⁷.

Reproductive traits were investigated in five *D. melanogaster* studies^{13–15,20,21}. **Overwintering fecundity** was recorded in field cages held at temperate winter conditions near Melbourne¹³ and at tropical winter conditions in Cairns¹⁴. Rako *et al.*¹⁵ tested for the **maintenance of fertility** in males that have survived in

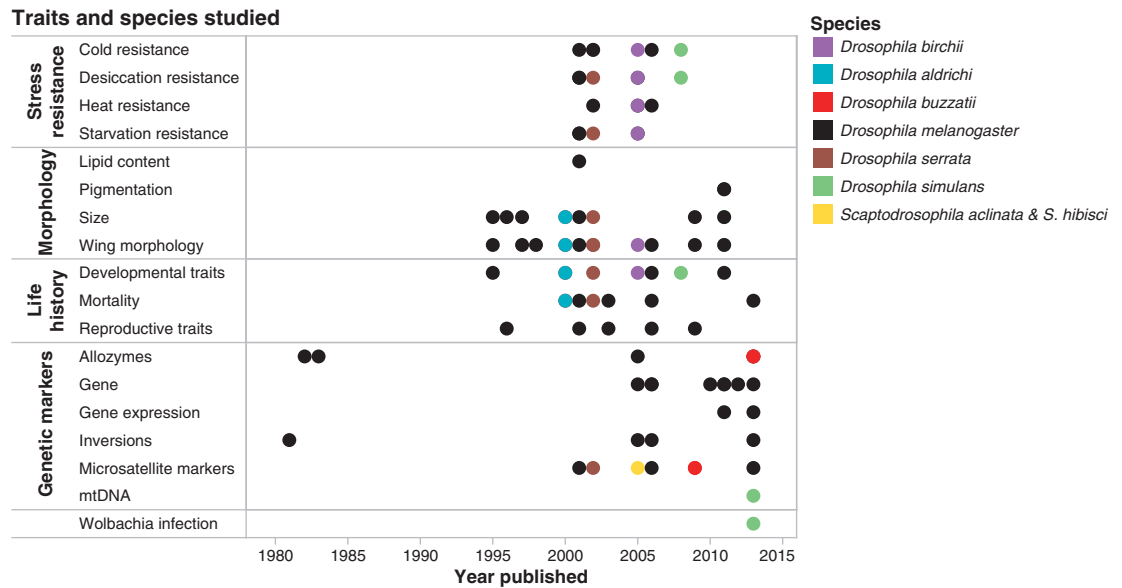


Figure 1. An overview of the trait groups and species studies in the datasets of ADEER. All datasets were published between 1982 and 2013 in a total of 39 papers.

field cages held at temperate winter conditions near Melbourne. Males were crossed to virgin females and the number of offspring was scored for each male¹⁵. **Ovariole number** was scored in two studies, whereas the number of ovarioles in each ovary was counted directly after dissection of the females^{20,21}.

Stress resistance traits

Sixteen datasets from 8 publications investigated stress traits in *D. melanogaster*, *D. serrata*, *D. simulans*, or *D. birchii*. These traits include cold resistance (8 datasets), desiccation resistance (6 datasets), heat resistance (4 datasets) and starvation resistance (5 datasets).

Cold resistance, scored as chill coma recovery time was investigated in *D. melanogaster*^{21,31}, *D. birchii*²³, *D. serrata*¹⁹ and *D. simulans*²⁸. Flies were placed in empty vials which were immersed in a 10% glycol solution cooled to a constant temperature of 0 °C. After 1–8 h, vials were removed from the cold bath and placed at room temperature and recovery time of flies was scored^{19,21,23,28,31}. Cold resistance scored as mortality after chill coma was investigated in *D. melanogaster*^{10,31} and *D. serrata*²⁷. Groups of females were placed into empty vials and submerged in a –2 °C waterbath for 1–3 h. Flies were allowed to recover in vials with fly medium for 24–48 h before scoring mortality^{10,27,31}.

Desiccation resistance was investigated in *D. melanogaster*^{10,32}, *D. serrata*¹⁹, *D. simulans*²⁸ and *D. birchii*²³. Flies were placed in empty vials covered with gauze and then transferred to a desiccator with silica gel left at 25 °C. Mortality was scored hourly until all flies had died^{10,19,23,28,32}.

Heat resistance was investigated in *D. melanogaster*^{21,31,32}, and *D. birchii*²³. Individual flies were placed into 5 ml glass vials submerged into a glass tank with water held at 39 °C (38.5 °C for *D. birchii*). Resistance was scored as the time taken for flies to be knocked down^{21,23,31,32}.

Starvation resistance was investigated in *D. melanogaster*^{10,32}, *D. birchii*²³ and *D. serrata*¹⁹. Flies were placed in vials/tubes containing agar and these vials were placed in a chamber with water to maintain humidity close to 100%. Chambers were held at 25 °C and mortality was scored at 6–8 h intervals until at least half the flies had died^{10,19,32}. Griffiths *et al.*²³ scored starvation resistance by placing flies in vials, which were then inverted over a second vial containing cotton wool and water. Flies in the vial were separated from the water with fine gauze and the two vials were sealed together with Parafilm®. The flies were scored for survival every hour until half the flies had died²³.

Genetic markers

This data collection contains 41 datasets from 20 publications that investigated genetic markers in *D. melanogaster*, *D. serrata*, *D. buzzatii*, *D. simulans*, *S. acclinata* or *S. hibisci*. Genetic marker types include allozymes (9 datasets), DNA sequence polymorphism (18 datasets), DNA repeat variation (i.e. microsatellites, 8 datasets), gene expression levels (4 datasets), inversion polymorphisms (5 datasets), and mitochondrial DNA regions (1 dataset).

Allozymes are enzymes that differ in electrophoretic mobility as a result of allelic differences at a single locus³³. Allozymes were investigated in *D. melanogaster*^{8,34–36} and *D. buzzatii*³⁷. Allozymes were scored after electrophoresis of single fly homogenates and staining^{8,34–37}. Adh and Pgd were scored

Species distributions

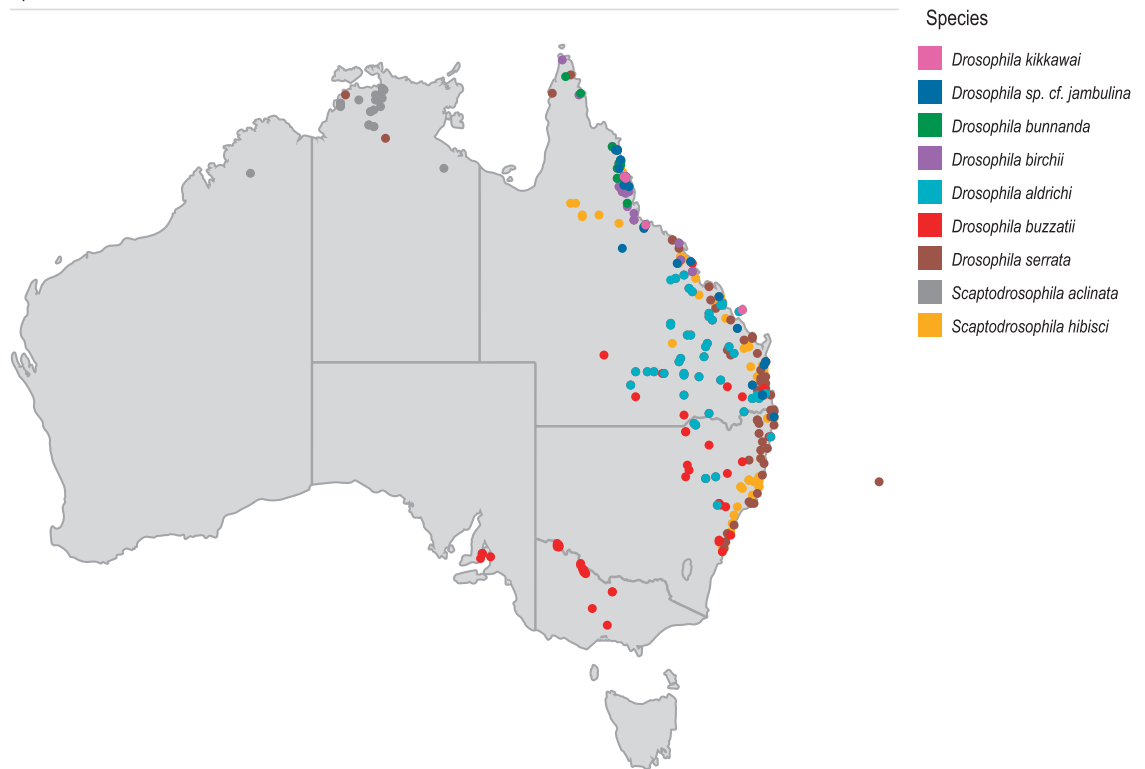


Figure 2. Collection records are shown for nine drosophilid species (*D. aldrichi*, *D. birchii*, *D. bunnanda*, *D. buzzatii*, *D. kikkawai*, *D. serrata*, *D. sp. cf. jambulina*, *S. acinata* and *S. hibisci*). These data were collected between 1924 and 2005 and are based on records in the literature, collections made by the dataset authors and specimens in the Australian Museum.

in *D. melanogaster*^{8,34–36} and *D. buzzatii*³⁷. Gpdh, G6pd and Pgd were scored in *D. melanogaster*^{35,36} and Aldox, Hex, Est1, Est2 and Lap were scored in *D. buzzatii*³⁷.

DNA sequence polymorphism can be determined using polymerase chain reaction (PCR) followed by gel electrophoresis (to detect size variation) or sequencing (to detect sequence variation)³³. *Drosophila melanogaster* has been intensively used as a model to study DNA sequence polymorphisms along the eastern Australian cline^{21,29,30,38–42}. In addition, variation in mitochondrial DNA sequences was investigated in *D. simulans*⁴³. Several genes have been investigated in *D. melanogaster*: *clock* and *period*⁴⁰, *couch potato*²⁹, *drosophila cold acclimation*³⁹, *frost*³⁸, *hsp70* (ref. 21), *hsr-omega*^{21,41}, *methuselah*³⁰, and *neurofibromin*⁴². The protocols to test for clinal variation in DNA sequence polymorphism varied substantially among the studies. In short, fly DNA was most often extracted using a Chelex/Proteinase K method⁴² but sometimes used a modified CTAB method⁴⁰. Amplification of nuclear and mitochondrial DNA was performed using standard PCR methods and variation in DNA sequences was determined by gel electrophoresis or sequencing. For further details see^{21,29,30,38–43}.

Microsatellites are tandemly repeated sequences of 1–6 nucleotides. Microsatellite markers are highly polymorphic and are assumed to evolve neutrally³³. Microsatellites were investigated in *D. melanogaster*^{22,34,41}, *D. buzzatii*⁴⁴, *D. serrata*²⁷, *S. acinata* and *S. hibisci*⁵. After DNA extraction, microsatellite markers were amplified by polymerase chain reaction (PCR) using the unique sequences of flanking regions as primers and then repeat length was measured either by separating radiolabelled products on a gel or separating fluorescent-labelled products on a DNA sequencer. For further details see^{5,22,27,34,41,44}.

Gene expression assays aim to quantify the level of RNA transcript present in the cell for each gene of interest using real-time PCR or deep-sequencing technologies⁴⁵. Expression of three genes was investigated in *D. melanogaster*: *couch potato*²⁹, *ebony*²⁵, and *methuselah*³⁰. In each case, RNA was isolated and purified to ensure DNA removal; cDNA was then synthesised for use as template for real-time PCR on the Light-Cycler[®] 480 (Roche) system and normalized using housekeeping genes. Further details are available in publications^{25,29,30}.

Inversion polymorphism refers to the phenomenon of a chromosome region appearing in either standard or ‘reversed’ orientation in a population, which results in multiple genes being inherited together rather than assorting independently. It has been intensively investigated in *D. melanogaster* in Australia. The inversion *In(3R)Payne* is the most frequently studied inversion^{8,41,42,46}, but *In(2R)NS*, *In(3L)Payne*, *In(3R)C*⁴⁶ and *In(2L)I*^{34,46} have also been investigated. Two different approaches were used to

test for inversion polymorphism: The BI-PASA method genotypes a SNP polymorphism shown to be in complete linkage disequilibrium with *In(3R)Payne* in Australia^{8,41,42}. Alternatively, a salivary gland preparation was made from a single 3rd-instar larva and lacto-acetic orcein was used to stain the chromosome. After staining, glands were squashed under a cover slip and visualized with a light microscope to examine banding patterns and loops characteristic of inversion status^{34,46}.

Wolbachia. *Wolbachia* are maternally inherited intracellular bacteria that can manipulate host reproduction⁴³. One study in this collection investigated *Wolbachia* infections in *D. simulans*⁴³. DNA was extracted using a standard Chelex based method and assays for *Wolbachia* infection status and strain type were performed with a fluorescence-based PCR assays using the Roche LightCycler[®] 480 system⁴⁷.

Species distribution collection

The species distribution collection contains data from two *Scaptodrosophila* species and seven *Drosophila* species (Table 1 (available online only), Table 3 and Fig. 2). Schiffer and McEvey⁷ investigated distributions of members of the *montium* subgroup (*Drosophila bunnanda*, *D. serrata*, *D. birchii*, *D. kikkawai* and *D. sp. cf. jambulina*) along the east coast of Australia. Collection records are available for 122 locations that were sampled between 1924 and 2005 and data are based on records in the literature, collections made by the authors and specimens in the Australian Museum⁷. Collection records are also available for the cactophilic *D. aldrichi* and *D. buzzatii*⁶. These species were sampled between 1971 and 2002 in 97 locations where *Opuntia* cacti occur and the *Opuntia* species were recorded for each location. Barker⁵ collected distribution data of *S. acinata* and *S. hibisci* which are both restricted to *Hibiscus* flowers⁵. *Scaptodrosophila acinata* were sampled in 24 locations in 1995 and *S. hibisci* were sampled in 63 locations in 1998 and the *Hibiscus* species were recorded for all locations. For further details see the relevant publications⁵⁻⁷.

Data Records

All 103 datasets are freely available through the ADEER website (<http://adeer.pearg.com/>), where additional datasets will be added in the future. In addition to the datasets, ADEER also provides a short description and a visualisation of each dataset and a link to the publication describing the datasets (Data Citation 1). The datasets can be accessed by browsing the collections, species or traits or by using the “Search” function. All 103 datasets are listed under “Browse Datasets” or as a default using the “Search” function. The data can be downloaded by clicking on the “Data Online” icon. A static version of all datasets was also transferred to Dryad on 19.7.2015 (Data citation 2). The datasets 63–70 from the Lee et al. (2011) publication are also freely available on the Dryad repository (Data Citation 3). In addition, the dataset 25 from the Lee et al. (2013) publication (Data Citation 4), the dataset 24 from the Kriesner et al. 2013 publication (Data Citation 5), the datasets 74–76 from the Sgrò et al. (2013) publication (Data Citation 6) and the datasets 37–39 from the Telonis-Scott et al. (2011) publication (Data Citation 7) are already freely available on the Dryad repository.

Technical Validation

All datasets of this collection have been published in peer-reviewed journals confirming the technical quality of the data and the appropriate use of experimental designs. Experimental designs always included control treatments where necessary and careful replication and randomization of the experimental units. All data have also been statistically analysed, which included testing for measurement and recording errors. Furthermore, in the process of collecting this resource, each dataset was visualized and checked for potential inconsistencies. Spelling mistakes were corrected in the datasets, but only datasets where no inconsistencies were found in the data were included in this resource.

Usage Notes

The annual average daily mean temperature of Australia has risen by 0.9 °C since 1910 (CSIRO 2014) and Australian temperatures are projected to continue to increase by about 2–4 °C by 2100 following the global trend⁴⁸. The increase in average and extreme temperatures presents a major challenge to biodiversity⁴⁹.

The clinal and species distribution datasets will be valuable for temporal comparisons in the future to understand current and future evolutionary responses to climate change and to predict species distributions under ongoing climate change scenarios. Clinal data of phenotypic traits and genetic markers as well as species distributions can be tracked over time and tested for adaptive responses under climate change⁸. In addition, researchers can use the datasets for comparing shifts in species distributions and linking these to climatic variables.

There is now ample evidence that natural populations are responding to climate change by shifting their geographic distribution and phenology^{50–52} and an increasing number of studies have demonstrated evidence for rapid adaptive evolution in response to climate change^{53,54}. Although plastic and genetic responses may allow some species to cope with climate change, extinction risks are predicted to be high, in particular in Australia⁵⁵. One major challenge is to identify the most vulnerable species that will not be able to adapt fast enough to keep pace with climate change^{52,53}. Collections like this one that span multiple related species with different degrees of adaptive potential and climate tolerance are important for understanding why some species are more vulnerable than others. Once this is better understood in

model groups like drosophilid flies, researchers can apply general patterns to mammals, birds, plants and other groups to help prioritise conservation efforts.

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Author Contributions

A.A.H. is the research sponsor of ADEER and is the main investigator of most of the data included in this resource. A.S. is the project manager of ADEER, P.C.G. is the research lead and SBH is a research data scientist of ADEER. All authors were involved in writing the paper.

Additional Information

Tables 1 and 2 are only available in the online version of this paper.

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