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Unusual suspects in the usual places: A phylo-climatic framework to identify potential future invasive species

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Running head: Identifying future invasive species

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ABSTRACT

A framework for identifying species that may become invasive under future climate conditions is presented, based on invader attributes and biogeography in combination with projections of future climate. We illustrate the framework using the CLIMEX niche model to identify future climate suitability for three species of Hawkweed that are currently present in the Australian Alps region and related species that are present in the neighbouring region. Potential source regions under future climate conditions are identified, and species from those emerging risk areas are identified. We use dynamically downscaled climate projections to complement global analyses and provide fine-scale projections of suitable climate for current and future (2070-2099) conditions at the regional scale.

Changing climatic conditions may reduce the suitability for some invasive species and improve it for others. Invasive species with distributions strongly determined by climate, where the projected future climate is highly suitable, are those with the greatest potential to be future invasive species in the region. As the Alps region becomes warmer and drier, many more regions of the world become potential sources of invasive species, although only one additional species of Hawkweed is identified as an emerging risk. However, in the longer term, as the species in these areas respond to global climate change, the potential source areas contract again to match higher altitude regions. Knowledge of future climate suitability, based on species-specific climatic tolerances, is a useful step towards prioritising management responses such as targeted eradication and early intervention to prevent the spread of future invasive species.

Keywords climate change, Hawkweeds, regional climate projections, species distribution models, weed risk assessment

INTRODUCTION

Biological invasions are regarded as one of the greatest current threats to global biodiversity (Millenium Ecosystem Assessment 2005). This threat is likely to change in the future, as species' distributions shift in response to changing climate conditions (Parmesan 2006; Parmesan and Hanley 2015; Root et al. 2003), introduction and dispersal patterns shift (Hellmann et al. 2008; Walther et al. 2009), productivity of native species declines (Catford et al. 2009), and the invasive potential of species changes (Gaskin and Wilson 2007; Nagel et al. 2004).

As the rates and patterns of invasion change, more proactive approaches may improve the outcomes of invasive species management. In the past, management of invasive species has tended to be reactive, with efforts being put into eradication attempts only after an introduced becomes invasive (Thuiller et al. 2007). However, the identification of potential future invasive species could help prevent establishment by reducing the likelihood of dispersal into an area (Gallien et al. 2010). Quarantine lists such as the Alert List for Environmental Weeds in Australia or the Federal Noxious Weeds List in the United States attempt to do this under current climate conditions.

A large body of literature has accumulated attempting to understand invasion processes and predict invasion success under current climate conditions (Catford et al. 2009; Guo 2006; Sutherst 2014). Several characteristics have been identified as being important, including the intrinsic properties of invaders, the susceptibility of natural communities to invasion, and biogeography, the documented distribution of a species in its native and invasive range (Auld et al. 2012). Invader attributes include functional traits such as reproductive strategies, dispersal, ability to hybridise, levels of phenotypic plasticity and genetic adaptation, and phylogeny. Phylogeny is an important attribute because being related to other invasive species may indicate the potential for invasiveness in the absence of species-specific knowledge (McGregor et al. 2012). Biogeography can indicate the relationship between invaders' distributions and environmental factors, and thus the extent to which a species' distribution is determined by climate (Guo 2006).

1 Consideration of these factors forms the basis of the Australian Weed Risk Assessment
2 (WRA) protocol (Pheloung et al. 1999), which has been adapted for application around the
3 world (eg. in the United States (Koop et al. 2012), Italy (Crosti et al. 2010), Japan (Nishida et
4 al. 2009) and New Zealand (Kriticos 2012b)). WRAs consider a species' biology,
5 biogeography, environmental preferences and known invasive tendency to determine the risk
6 that it will become invasive if introduced to a new location. The score from such assessments
7 is used to decide on appropriate management and quarantine restrictions. Similar approaches
8 are used in Pest Risk Assessment protocols around the world (Eyre et al. 2012).

11 Several recent studies have modelled the effect of changing climate conditions on individual
12 (eg. Bradley et al. 2010a; Kriticos et al. 2015a; Kriticos et al. 2003; Taylor et al. 2012), and
13 multi-species groups of invasive species (Bellard et al 2013; Crossman et al. 2011; Gallagher
14 et al. 2013; Gritti et al. 2006; Roger et al. 2015). Our objective in this paper is to develop a
15 general framework for identifying species that may become invasive (sensu Mack et al. 2000)
16 under future climate conditions. By following the framework we identify future climate
17 suitability for:

- 18 1. Introduced species that are currently present in the area of interest;
- 19 2. Related species that may be absent now from the area of interest, but are present in
20 the neighbouring region; and
- 21 3. Related species that are not currently present in the region, but are found in areas of
22 the world with a similar climate to that projected for the future in the region of
23 interest.

24 We illustrate the framework using a case study of Hawkweed species (*Hieracium* spp.) in the
25 Australian Alps region. The same approach can be applied to any species or region of the
26 world.

27 **METHODS**

28 *Case Study*

29 The Australian Alps are likely to be highly susceptible to climate change (Hughes 2011). The
30 region has warmed at a rate of about 0.2 °C per decade over the past 35 years (Braganza et al.
31 2015). Under a business as usual (high) emissions scenario (RCP 8.5), average temperatures

are projected to increase by 4-5°C and rainfall is projected to decline by 5-20% (Climate Futures for Australia projections, <http://cfa0.rdsi.tpac.org.au/thredds/catalog.html>). These rates of increase are higher than the observed and projected increases in the global mean temperature (observed increase 0.12 °C per decade since 1951; projected increase 2.6-4.8 °C relative to 1986-2005 (IPCC 2014)).

The Hawkweeds are a diverse group of perennial herbs, with almost 1 000 species recognised globally (International Organization for Plant Information 2015). Their biogeography suggests that they are highly adapted to a variety of environmental conditions, such as nutrient availability, soil type, slope and aspect, and there are few biotic interactions that restrict growth and reproduction. They produce large numbers of wind-dispersed seeds and produce allelochemicals that inhibit the growth of other plants (Williams and Holland 2007). In addition to reproducing sexually or apomictically (ie. by producing seeds without fertilisation), species belonging to the *Pilosella* sub-genus also reproduce asexually by means of stolons (Makepeace 1985). These reproductive and dispersal traits suggest high invasive potential. In contrast, there are two non-stoloniferous sub-genera, *Chionoracium* and *Hieracium sensu stricta*, which only reproduce sexually (Williams and Holland 2007).

No *Hieracium* species are native to Australia. Four species (*H. aurantiacum*, *H. pilosella*, *H. praealtum* and *H. murorum*) have become naturalized in south-eastern Australia, although they are not widespread. These species are from Northern Europe, and have become highly invasive in the United States, Canada, New Zealand and Japan. *Hieracium aurantium* (syn *Pilosella aurantiaca*), *H. pilosella* (syn *Pilosella officinarum*) and *H. praealtum* (syn *Pilosella piloselloides*) belong to the *Pilosella* group, while *H. murorum* belongs to the non-stoloniferous *Hieracium* group. Orange Hawkweed (*H. aurantiacum*) is currently the species of most concern in the Australian Alps, with the potential to become widely established and threaten native biodiversity. However, all species of *Hieracium* are now listed as noxious or prohibited weeds in Australian state legislation (Natural Heritage Trust 2003).

Analytical Framework

Figure 1 outlines the framework to identify potential future invasive plant species in a region.

Step 1: For introduced species currently present in the area of interest, we ask the following questions:

- A. Is the species invasive known to be invasive anywhere in the world? If not, it is considered unlikely to become invasive in the future. If the answer is yes, we ask:
 - B. Is the species' range strongly determined by climate? This is assessed by considering the biogeography of the species, in both the native and introduced range (see Methods section). Where the extreme range boundaries cannot be modelled using biologically valid climate parameters (for example, the observed range remains substantially smaller than the modelled range), factors other than climate may be restricting the current distribution. These species may have the potential to become future invasive species, but their response to site environmental characteristics are not predictable. For species whose ranges do appear to be climatically driven, we ask:
 - C. Is the future climate suitable? If not, the species is considered unlikely to be widespread invasive species under future conditions, although local persistence may be possible in favourable microhabitats or resulting from plasticity or adaptation to the new conditions.
- Species for which the answer is yes to all questions are considered to have potential to be future invasive species in the region under a changing climate.

Step 2: For related species present in the neighbouring region that are currently absent from the area of interest, the same questions (A, B and C) are applied.

Step 3: For related species with potential to be introduced in the future, we ask:

- A. Is the species' native range climatically similar to the projected future climate of the region? If not, it is considered unlikely to become invasive in the future. If it is similar, we ask:
- B. Does the species have invasive attributes? If not, we ask:
- C. Is the species related to any invasive species? If the answer to the two preceding questions is yes, we ask:
- D. Is the future climate suitable? Only if the future climate is suitable is the species considered to have the potential to become invasive in the future.

For species for which the answer is yes, the pathway then follows the same questions about invasiveness and relatedness to invasive species as above.

Uncertainty

Attempts to identify future invasive species must explicitly acknowledge and analyse the uncertainty inherent in attempts to project biological responses to future conditions (Gould et al. 2014; Venette et al. 2010; Yemshanov et al., 2013). There are three main sources of uncertainty in projections of future climate: future emissions scenarios, the uncertainty represented by the range in climate models, and the internal variability of the climate system. Of these, the greatest sources of uncertainty in the short term are model uncertainty and internal variability, while the importance of uncertainty associated with emissions scenarios increases in the longer term (Harris et al. 2014). These sources of uncertainty are then compounded by uncertainty in the species distribution models, which can be affected by the choice of statistical model (Buisson et al. 2010; Pearson et al. 2006), the parameters chosen within the model (Merow et al. 2013); the environmental variables used to define the niche (Beaumont et al. 2005; Harris et al. 2014; Synes and Osborne 2011), and bias in locality data (Beaumont et al. 2009; Barry and Elith, 2009). We present a general framework for identifying future invasive species that can be applied using a range of modelling approaches, but the sources of uncertainty will vary depending on the modelling approach.

Modelling climate suitability using the CLIMEX model

Current and future climate suitability for each species was modelled using CLIMEX version 4 (Kriticos et al. 2015b). CLIMEX is a species niche model which is based on the assumption that it is possible to infer a species' climatic tolerances from its current distribution. Superficially, it appears similar to other species distribution models (SDMs), however, where correlative SDMs characterise the environment in which a species is known to occur, CLIMEX describes how the species responds to climatic variables at weekly time scales (Kriticos et al. 2015b). It does this using parameters that describe a species' response to temperature, soil moisture and light to calculate population growth and stress indices. CLIMEX defines range boundaries using climatic stress factors that are generally inferred from the known geographical distribution of the species, in accordance with ecological theory on range constraints (Brown et al. 1996). The stress functions can be informed by

experimental data or phenological observations when such information are available (Kriticos et al. 2015b). Within the range boundaries, a species' climate suitability is modelled in terms of temperature and soil moisture response functions following the Law of Tolerance (Shelford 1963), combined in accordance with the Law of the Minimum (reviewed in van der Ploeg et al. 1999). The model fitting process in CLIMEX differs from the linear methods generally used to fit species distribution models because the method of multiple working hypotheses is used to consider information across knowledge domains (distribution data, experimental observations, phenology, biological theory) (Chamberlin 1965). Because they do not rely solely on distribution data, CLIMEX models tend to be remarkably robust, especially when projecting results into novel climate situations such as species invasions of new continents, and into future climate scenarios (Sutherst and Bourne 2009; Webber et al. 2011). The stress functions are fitted to the most climatically extreme range records, so, assuming sufficient spatial coverage of observations exists to cover the major climatic gradients, sampling bias is minimised. Combining knowledge of distribution data, experimental observations and biological theory helps protect against problems of incomplete sampling of the range of the species being modelled and misinterpretation of presence records.

For each climate station, weekly Temperature and Soil Moisture growth indices are calculated and integrated into an annual growth index, scaled from 0 to 100, where 100 indicates perfect conditions throughout the year. The weekly indices describe the weekly suitability of the climate for development, reproduction and survival, while the annual growth index describes the overall potential for growth as determined by climate alone. These indices determine the Ecoclimatic Index (EI), which can be interpreted in a similar way to the occurrence probability in correlative SDMs to determine the species potential distribution under current and future climate conditions. However, the EI differs in that it incorporates the species' growth and stress responses to temperature, moisture and light to indicate how suitable the conditions at a point are for population growth and persistence. It is also scaled between 0 (unsuitable) and 100 (climatically perfect all year round). Full equations for all CLIMEX indices can be found in (Sutherst and Maywald 1985) and (Kriticos et al. 2015).

Here we parameterised CLIMEX models by fitting stress functions to the native range of each species, and validated the results by checking that the invasive range was captured by

the model. The resulting stress maps for each species are presented in Supplementary Material S1.

Species records were obtained from the Global Biodiversity Information Facility (GBIF) (<http://www.gbif.org/>), and the Atlas of Living Australia (<http://www.ala.org.au>), and cover the years 1844 to 2014. The number of records from the GBIF and ALA respectively for each species were: *H. aurantiacum* (3, 165;101); *H. pilosella* (160, 178; 52); *H. murorum* (175,544; 24); *H. praealtum* (58, 44). These records were supplemented by shapefiles of treatment areas within the Australian Alps region provided by Alps managers. The global distributions of the four Hawkweed species currently in Australia are shown in Supplementary Material S2 (Figures S2.1 and S2.2). Locality data are provided in Supplementary_data_S2.

CLIMEX parameters for the Hawkweed models

The CLIMEX parameters for the species differ slightly to capture their native range and account for differences in phenology (Table 1). The same parameters were used for *H. pilosella* and *H. murorum* because they have very similar recorded distributions in both their native and introduced ranges, indicating that non-climatic factors likely determine their niche differentiation. The optimum temperatures for these species are lower than for the other species, reflecting their wider, more northerly European distributions, and because they flower for several months longer than *H. aurantiacum* (Kuhn et al. 2004). The model for *H. aurantiacum* includes a hot-dry interaction stress term to restrict the native range model in Europe from extending south into the warmer and drier region of Spain. This also improved the representation of its distribution within Australia and on the east coast of North America. *Hieracium praealtum* has a highly restricted native distribution, represented by only 58 reliable records in the GBIF database (compared to many thousands of records for the co-occurring *Hieracium* species). The final parameters selected suggest an area of climate suitability that extends beyond the observation points, from southern France, north to Denmark and as far east as Hungary.

A sensitivity analysis was done to assess the influence of each variable on the model results, and identify those variables of most concern in terms of accuracy. Overall, the Range change (the percentage of locations whose EI changes about the threshold value), and patterns in

Ecoclimatic Index and Core Distribution (a summary variable indicating the absence of stresses) were relatively insensitive to the model parameters, particularly in the cases of *H. aurantiacum* and *H. praealtum*. *Hieracium pilosella* and *H. murorum* showed slightly higher parameter sensitivities, with the highest value of 7.8% (for the effect of Dry Stress threshold (SMDS) on the Ecoclimatic Index). Although this parameter is relatively sensitive, we have high confidence in its accuracy, because it is based on known physiological limits to plant growth under dry conditions. The results are presented in Supplementary Material S3.

To assess parametric model uncertainty, we generated maps showing the proportion of model runs (n=100) where the models agreed that the climate was suitable for each species of Hawkweed (ie. Ecoclimatic Index above zero). The results of the uncertainty analysis (shown in Supplementary Material S4) indicated that there is a high level of model agreement around the areas identified as being climatically suitable for establishment of all species, increasing confidence in the models of potential distributions.

Regional climate matching in CLIMEX

Regional climate matching in CLIMEX compares the long-term meteorological data for the set of *away* locations with the climate of the stations in the *home* region, without reference to any particular species. The level of similarity is given by the Composite Match Index (CMI), the product of up to six component indices representing similarity in maximum and minimum temperature, total rainfall, rainfall pattern, relative humidity (RH) and soil moisture. Each component index ranges from 0 to 1, and can be weighted individually to emphasise more important variables. We calculated the CMI based on weekly maximum and minimum temperature, annual rainfall and annual rainfall pattern (equal weightings of 1.0 and zero for RH and soil moisture). A value of 1 indicates an exact match with at least one station in the *home* region, and values of 0.7 or greater indicate a climatic match that is worthy of consideration in terms of biological similarity. The calculations used to derive the Composite Match Indices are given in Supplementary Material S5.

The regional climate matching procedure in CLIMEX was used to identify regions of the world from which future invasive species may come, using two methods. The first method

covers the likelihood that changes to some species distributions in their native ranges will lag behind changes to climate. We modelled this by matching the future climate of the Australian Alps region (the *home* locations in CLIMEX) with current climate conditions in the University of East Anglia's Climatic Research Unit (CRU) world dataset (the *away* locations) (data available from <https://www.climond.org/ClimateData.aspx>). The second method accounts for the fact that climate will be changing around the world over the next century, and is modelled by matching the future climate of the Alps with future world conditions (Kriticos 2012a).

Identification of new invasive species under current and future climate

All records of all species belonging to the *Hieracium* and *Pilosella* genera were downloaded from the Global Biodiversity Information Facility (GBIF) (335,446 records), and species lists generated for current risk areas (current world with current Alps) and emerging risk areas (current world with future Alps).

Climate data

Two different datasets were used to provide i) global and ii) fine scaled regional climate data. The global data were necessary to parameterise the CLIMEX models based on the native European ranges as well as match climates from regions around the world with the Australian Alps at different time periods. The regional climate projections provide fine resolution projections of future climate suitability at a scale relevant for invasive species management. The framework is applicable regardless of the projections used, including simply scaled climate data such as WorldClim (Hijmans et al. 2011) that are commonly used in ecological studies.

i) Global analyses

The CLIMEX models were parameterized using the historical climate data from the CliMond CM10 dataset (Kriticos et al. 2012b). This dataset is a hybrid of monthly minimum and maximum temperature, monthly precipitation from Worldclim (Hijmans et al. 2011) and mean relative humidity from the University of East Anglia's Climatic Research Unit (CRU) CL1.0 1961-1990 reference climatology, at a resolution of ~18km (Mitchell and Jones 2005). The CliMond dataset also provides worldwide projections of future climate based on output

from models in the Coupled Model Intercomparison Project archive (CMIP3), which provided the science basis for the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change. Models from the most recent model archive (CMIP5), which underpins the science of the Fifth Assessment Report (AR5) (IPCC, 2014), will be added to the CliMond dataset in 2016. The CMIP archives include a standard set of model simulations that have been assessed as providing plausible projections of future climate change. See Harris et al. (2014) for an overview of climate model outputs and issues that need to be considered when applying projections of future climate in ecological studies.

We present results for the end of century (hereafter 2080) based on the CSIRO Mk3.0 and MIROC3.2.hires global climate models (GCMs) under the high emissions scenario (A2), also at a resolution of 10 arc minutes (~18 km). These models were chosen because they represent a range from a cool and dry future (CSIRO Mk3.0), to a warm and wet future (MIROC3.2.hires), relative to the CMIP3 archive mean. These datasets were also used for the regional climate matching analyses.

ii) Regional analyses for the Australian Alps

Dynamically downscaled climate projections were used to provide fine-scaled future climate data at ~5km resolution over the Alps. Results are presented for three Global Climate Models (GCMs) from the Coupled Model Intercomparison Project archive (CMIP5) that were dynamically downscaled using the Conformal Cubic Atmospheric Model (CCAM). The host models, ACCESS-1.0, MPI-ESM-LR and NorESM1-M, were chosen to represent a range of plausible future climates. NorESM1-M projects the lowest temperature increases over the region (approximately 3°C) and an increase in precipitation of 13% by the end of the century, while ACCESS-1.0 and MPI-ESM-LR project a drier and warmer future (decreased precipitation of 5% and temperature increases of ~5°C by the end of the century). Details of the CCAM model can be found in (Corney et al. 2013), and the modelled projections are available through the Tasmanian Partnership for Advanced Computing (TPAC) portal (<http://cfa0.rdsi.tpac.org.au/thredds/catalog.html>). We present results for the high emissions scenario (RCP 8.5).

In contrast to statistical downscaling methods, which assume a statistical relationship between large-scale patterns of climate and local climate, or simple scaling techniques that

interpolate coarse-scale model output to the local scale, dynamically downscaled models represent the physical processes that operate over small distances (Harris et al. 2014). They therefore have the potential to capture regional variation in the climate change signal, particularly in regions of complex topography such as the Alps. However, due to the very high computational requirements of dynamical downscaling, these models can only be practically run over relatively small regions.

The CMIP5 archive includes different climate models, and Representative Concentration Pathways (RCPs) rather than the SRES emissions scenarios used in the CMIP3 archive, from which the worldwide climate data were taken. The results based on the fine-scale regional data are therefore not directly comparable with the results based on the worldwide climate data, although broad trends can be compared since they all represent plausible future climate conditions under a high emissions scenario. RCP8.5 projects a similar acceleration in temperature to SRES A2, although median temperatures are consistently higher in the RCP8.5 (Rogelj et al. 2012). The global temperature changes projected in the CMIP5 archive are very similar to those in the CMIP3 archive once the different scenarios are taken into account (Knutti and Sedlacek 2013). Regional comparisons of projections from the CMIP5 and CMIP3 models have also found surface temperature, wind, and rainfall patterns to be highly consistent between the archives (Irving et al. 2012; Lee et al. 2013). The release of the CMIP5 archive models has therefore not made the CMIP3 models redundant (Harris et al. 2014).

RESULTS

STEP 1: Introduced species currently present

Hieracium aurantiacum (Orange Hawkweed). This is a typical alpine species, found up to 2800m in altitude in its native range (northern, central and Eastern Europe). Its invasive range currently includes parts of North America, Japan, New Zealand and Australia. The current climate of the Australian Alps is suitable for this species, but suitability declines under future climate conditions (Figure 2a). By the end of the century, the climate over the Alps is projected to have warmed and dried so that very few, if any, areas are projected to remain suitable. The results from the two climate models differ slightly, mainly in the rate at which areas of the Alps became unsuitable for this species. By 2080, the CSIRO Mk3.0 model

projected no suitable climate, while MIROC3.2.hires projected a small localised area remaining suitable in the southern Alps.

Hieracium pilosella (Mouse Ear Hawkweed). This species is native to Europe and northern Asia, extending further south than *H. aurantiacum* into warmer and drier regions (eg. Spain). It is invasive to New Zealand and North America. The current climate is suitable for this species and remains suitable across most of the Alps region by the end of the century, although the extent of suitable climate across southern Australia contracts substantially (Figure 2b). The two climate models again produced slightly different extents of suitable climate under future conditions, with the wetter model, MIROC3.2.hires, projecting a greater area in south-eastern Australia remaining highly suitable by 2080.

Hieracium praealtum (King Devil Hawkweed) has been found in small areas within the region. The suitability of the Alps under current and future climate is low for *H. praealtum* (Figure 2c). However, the process of developing the CLIMEX model highlighted that climate may not be the primary limiting factor for this species, because it was not possible to capture the highly restricted native distribution with biologically plausible combinations of parameters. Consideration of biogeography and its recent invasiveness in New Zealand suggest that this species does have the potential to become invasive in the Australian Alps, and its response to future climate conditions is difficult to estimate.

STEP 2: Related species absent now, but present in the neighbouring region

Hieracium murorum (Wall Hawkweed) is currently absent from the Alps region, but has been recorded in south-eastern Australia. The future climate is projected to remain suitable for *H. murorum* (Figure 2b). However, this species is less invasive than the other species examined here, and is non-stoloniferous, so follows a different pathway within the framework. This results in it being placed towards the right hand side of the decision pathway, considered to have lower potential to be a future invasive (Figure 1).

STEP 3: Related species with potential to be introduced

The regions of the world that are currently climatically similar to the Australian Alps include New Zealand, Northern Europe, eastern United States, and the higher elevation regions of

Western Europe, southern Africa, South America and China. A map and a list of Hawkweed species currently distributed in these areas are listed in Supplementary Material S6. In the future, the climate of the Alps is projected to match more regions of the world at lower altitudes (matching future Alps climate with current climate conditions across the world). Northern Africa and parts of Central Asia become climatically similar, as do more extensive areas of Australia and southern Africa. Changes to source areas under climate change are identified in the composite map in Figure 3. The MIROC3.2.hires model projects fewer emerging source areas, and larger areas of Northern Europe to be declining risk areas, compared to the CSIRO Mk3.0 model, which projects greater areas to match the Alps climate in the future.

Overlaying the new source areas with locality records of all Hawkweeds identified one additional species (*H. pringlei*) that may emerge as a potential threat in the future, regardless of which climate model was used. Matching the climate of the current native range with the future Alps climate leads to an increased geographic area because the future Alps climate is more similar to warmer, lower elevation areas (Figure 4b). This result identifies potential future threats, assuming there will be a lag in the response of species to changing climate in their native range. In the long term, however, as species respond to changing climate conditions in their native ranges, potential source regions contract again, although the area remains larger than under current climate conditions. Under the scenarios considered here, higher elevation regions of China, South America and southern Africa, in addition to much of the United States and Western and Northern Europe are projected to be climatically similar to the Alps by the end of the century (Figure 4c).

Regional analyses for the Australian Alps

The finer resolution in the downscaled climate models highlights regional differences in suitability for each of the species (Figures 5 -7). Climate suitability for *H. aurantiacum* is projected to substantially decline across south-eastern Australia by the end of the century. One climate model (MPI-ESM-LR) projects no suitable climate remaining, but in contrast to the broad-scale analysis, the two other models (ACCESS-1.0 and NorESM1-M) project small areas of suitable climate at the highest elevations. Climate suitability in these areas increases under the NorESM1-M projections.

1 The regional analysis for *H. pilosella* and *H. murorum* suggests that climate suitability will
2 decline across south-eastern Australia, as is suggested by the broad-scale analysis. However,
3 the 5km resolution data highlights the patchiness of highly suitable climate across the Alps
4 region, again strongly driven by altitude and aspect. Coastal and inland areas to the east of the
5 Alps are generally marginal or unsuitable in all models, with the Ecoclimatic Index
6 increasing with altitude. The Wilsons Promontory area is the exception with climate
7 remaining highly suitable in all models.
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10 Climate suitability for *H. praealtum* is currently low across the Alps except in localised high
11 elevation areas. Suitability is projected to decline under the ACCESS-1.0 and MPI-ESM-LR
12 models and increase under NorESM1-M.
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16 **DISCUSSION**

17 The interaction between climate change and biological invasions is likely to present an
18 ongoing challenge into the future. A comprehensive turnover of species can be expected to
19 occur in the Australian Alps, requiring a shift in the current management paradigm (Dunlop
20 et al. 2013; Harris et al. 2015). Regardless of the mode of introduction (Hoffmann and
21 Courchamp 2016), invasions from lower altitudes will be a natural response to the changing
22 climate, displacing colder-adapted species as their climate suitability declines. These
23 invasions will inevitably comprise a mix of native and exotic species adapted to the warming
24 conditions. Decisions will need to be made about which species are acceptable, and which
25 should be prevented from establishing.
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28 Currently established invasive species for whom the projected future climate is highly
29 suitable are those that have the greatest potential to be future invasive species in the region
30 (eg. *H. pilosella*). In contrast, species for whom climate suitability is projected to decline (eg.
31 *H. aurantiacum*) may be of less concern in the future, although suitable microclimates may
32 remain in areas with high topographic diversity (Dobrowski 2011). Related species that are
33 currently absent but have potential to disperse from the neighbouring region have the most
34 immediate potential to spread up into the higher altitude areas. Species that are not currently
35 invasive are of less concern, but if they are related to invasive species or possess invasive
36 attributes, they may still have potential to become invasive in the future. For example, *H.*
37 *murorum* is a non-stoloniferous species that is not highly invasive, so is considered to have
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less potential to become invasive under future climate conditions compared to the stoloniferous species. On the other hand, considering its phylogenetic relationship to other highly invasive Hawkweed species, it may still be prudent to take steps to prevent its establishment. Species whose global distribution suggests that factors other than climate are strong influences may have the potential to be invasive in the future, but their response to site environmental characteristics is less predictable under future climate conditions. *H. praealtum*, for example, has a very restricted native range, but is highly invasive in New Zealand, suggesting that biotic factors such as release from congeneric competitors and fungal attack, and/or hybridization are important in determining future invasiveness in this species.

There have been many studies that have used SDMs to project the suitability of future climate conditions for species that are currently invasive (eg. Bradley et al. 2010a), but fewer studies look at closely related species. We include relatedness to a known invasive to cover species that may never have been introduced outside their native range. In New Zealand, for example, more than 20% of recently naturalised introduced plants have no history of invasion elsewhere in the world (Williams et al. 2000). Additionally, there is greater potential for hybridisation to occur between related species, as appears to have happened in the case of *H. praealtum* in New Zealand, where it has become far more invasive than would be expected from its very limited native range (Morgan-Richards et al. 2004).

Regional climate matching is a useful approach for “horizon scanning” (Roy et al. 2014) to identify potential source regions under future climate conditions (Kriticos 2012b). There are more than 900 accepted species of Hawkweed globally (International Organization for Plant Information 2015), with distributions spanning a range of climate zones. While the origins of the three subgenera are different, with *Chionoracium* originating in North America, and *Hieracium* and the more invasive *Pilosella* subgenera centred on Eurasia, they have all spread widely around the world. For example, of the 36 *Hieracium* species currently found within North America north of Mexico (Strother 2006), thirteen are introduced from Eurasia (Gaskin and Wilson 2007). We identified seventy species of Hawkweed currently distributed in regions with similar climates to the Alps, and one additional species was identified as having the potential to emerge as an invasive species in the future. This species, *H. pringlei*, is native

to Central America, and is listed as a noxious weed in the North American state of Washington.

The species currently of concern originated in the European mountains. By the end of the century, the climate of the Alps will be warmer and drier than these higher elevation areas have been historically, so species which are currently only found in the colder regions of Northern Europe (eg. *H. caespitosum*, *H. caesium*, *H. hjeltii*) (Tyler 2014), may be of less concern in the future. The area from which invasive species may originate will increase in the medium term, because there will be a lag between the global climate changing and the response of species (Kriticos 2012b). As the Alps become warmer and drier, many more regions of the world become potential sources of invasive species. Northern Africa and parts of Central Asia are projected to become new source regions, as are more extensive, lower elevations areas of southern Africa, Australia and South America (see Figure 3). However, in the longer term, as the species in these areas respond to global climate change, the potential source areas will contract again. The higher elevation regions of China, South America and southern Africa, in addition to much of the United States and Western and Northern Europe, are most likely to be the future source regions for invasive species into the Australian Alps.

The analyses based on the regional climate model provided finer resolution results relevant to the scale at which invasive species management occurs. Many millions of dollars are currently spent annually in the Alps region attempting to reduce the establishment and spread of invasive plant species, including Hawkweed species, Broom species (*Cytisus* spp. and *Genista* spp.) and Willow species (*Salix* spp.) (Sainty et al. 2007). These results could be used to prioritize weed management in several ways. Species that may currently have a limited distribution in the region could be eradicated early if the future climate is projected to become more suitable. Targeted searches for new invasive species could be carried out in areas identified as being at higher risk of becoming climatically suitable for that species. Quarantine restrictions could be applied to prevent the importation of species from regions with climates similar to that projected to occur in the Alps region in the future. Resources could be redirected from those species with declining climate suitability towards species that are identified as being invasive in the future.

Understanding where species may be invasive in the future is subject to a great deal of uncertainty. While many of these sources cannot be eliminated, an understanding of

1 uncertainty and its sources will lead to better decision-making. The range in climate models
2 is an important source of uncertainty that must be considered. In our case study, the CSIRO
3 Mk3.0 model projected no suitable climate for *H. aurantiacum* remaining by 2080, while
4 small areas remain suitable under the MIROC3.2.hires projections. CSIRO Mk3.0 produces a
5 future that is cooler and drier than the CMIP3 archive mean, while MIROC3.2.hires is
6 warmer and wetter ([http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-chapter11-](http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-chapter11-supplement.pdf)
7 [supp-material.pdf](http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-chapter11-supplement.pdf)). In the regional analyses based on the CMIP5 climate models, NorESM1-
8 M projected greater areas of suitable climate for all species compared to the other climate
9 models. This model projects increased precipitation of 13% in the region at elevations above
10 500m, in contrast to the other two models which project reductions in precipitation of 6% (by
11 the end of the century, relative to 1961-1990). Rainfall projections typically have a larger
12 degree of uncertainty than those for temperature, because it is difficult to fully resolve the
13 many physical processes or the fine-scale spatial variability involved in precipitation (Dowdy
14 et al. 2015), and the large-scale storm tracks in the projections are uncertain (Risbey and
15 O’Kane 2011). For this reason it is not unusual for projections of rainfall change in a region
16 to range from positive to negative (CSIRO and Bureau of Meteorology 2015). However, all
17 models admitted to the archive are considered plausible, and capture the climate processes
18 and circulation well over south-eastern Australia. It is therefore not possible to select one
19 model over another, and results based on multiple climate models should be considered to
20 frame the range of plausible futures (Harris et al. 2014). It is also worth considering how the
21 differing degree of uncertainty in climate variables might affect models of future climate
22 suitability for species limited by different climate variables.
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39 Similarly, the uncertainty due to the choice of species distribution model and its
40 parameterisation should be assessed and incorporated into decision-making. Species
41 distribution models of invasive species based on ‘climate envelopes’ are designed to estimate
42 the realized distribution of a species well, but their ability to estimate the potential
43 distribution, especially in novel environments is limited by the difficulties of incorporating
44 important factors such as dispersal, species interactions, plasticity or genetic adaptability
45 (Brooker et al. 2007; Hulme 2003). The process of developing the CLIMEX model for
46 *H.praealtum* highlighted the limitations of climate modelling when a species’ distribution is
47 constrained by a non-climatic factor such as competition (Nunez and Medley 2011). By using
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the CLIMEX model within a framework that considers biogeography in the native and introduced ranges, phylogeny and other invader attributes, we have attempted to reduce these limitations.

CONCLUSIONS

The analytical framework demonstrated here is an extension of current weed risk assessment procedures to assess the potential for future invasiveness under climate change, and is applicable to any region or taxon of interest. Considering invader attributes and biogeography, in combination with projections of future climate suitability, provides an assessment of the likelihood of future invasiveness of introduced species that are currently present in an area, as well as species that have the potential to be introduced. This method ensures that present day strategic plans to manage invasive species are likely to be robust in the face of a changing climate.

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Table 1: CLIMEX model parameters used for *Hieracium* species

	<i>H. aurantiacum</i>	<i>H. pilosella,</i> <i>H. murorum</i>	<i>H. praealtum</i>
Temperature Index			
Limiting Low Temperature (DV0)	0	0	5
Lower Optimal Temperature (DV1)	20	15	20
Upper Optimal Temperature (DV2)	25	20	25
Limiting High Temperature (DV3)	30	30	30
Moisture Index			
Limiting Low Moisture (SM0)	0.12	0.12	0.2
Lower Optimal Moisture (SM1)	0.34	0.34	0.6
Upper Optimal Moisture (SM2)	1.7	1	1
Limiting High Moisture (SM3)	2.5	2.5	2
Light Index	Unused	Unused	Unused
Diapause	Unused	Unused	Unused
Cold Stress			
<i>Minimum Temperature</i>			
Cold Stress Temperature Threshold (TTCS)	-20	-20	-5
Cold Stress Temperature Rate (THCS)	-0.01	-0.01	-0.05
<i>Degree-Days above Threshold</i>			
Cold Stress Degree-Day Threshold (DTCS)	0	0	5
Cold Stress Degree-Day Rate (DHCS)	0	0	-0.005
<i>Average Temperature</i>			
Cold Stress Temperature Threshold (TTCSA)	0	0	0
Cold Stress Temperature Rate (THCSA)	0	0	0
Heat Stress			
<i>Maximum Temperature</i>			
Heat Stress Temperature Threshold (TTHS)	34	34	Unused
Heat Stress Temperature Rate (THHS)	0.08	0.08	Unused
<i>Degree-Days above Threshold</i>			
Heat Stress Degree-Day Threshold (DTHS)	50	50	Unused
Heat Stress Degree-Day Rate (DHHS)	0	0	Unused
Dry Stress			
Dry Stress Threshold (SMDS)	0.085	0.085	0.14
Dry Stress Rate (HDS)	-0.6	-0.6	-0.07
Wet Stress			
Wet Stress Threshold (SMWS)	Unused	Unused	2
Wet Stress Rate (HWS)	Unused	Unused	0.01
Cold-dry Stress	Unused	Unused	Unused
Cold-wet Stress	Unused	Unused	Unused
Hot-dry Stress			
Hot-Dry Temperature Threshold (TTHD)	25	Unused	Unused
Hot-Dry Moisture Threshold (MTHD)	0.5	Unused	Unused
Hot-Dry Stress Rate (PHD)	0.5	Unused	Unused
Hot-wet Stress			
Hot-Wet Temperature Threshold (TTHW)	26	26	Unused

Hot- Wet Moisture Threshold (MTHW)	0.7	0.7	Unused
Hot- Wet Stress Rate (PHW)	0.255	0.255	Unused
<i>Model time step</i>	7	7	7
<i>Degree-days per generation</i>	600	600	600

Figure 1: Framework to identify potential future invasive plant species

Figure 2: Ecoclimatic Index for four species of Hawkweed in Australia under historical and future (2080) climate conditions, based on two Global Climate Models using a high emissions scenario (SRES A2). Green areas (>60%) are optimal for growth and reproduction. Suitability declines towards zero.

Figure 3: Change in potential source areas projected by two climate models for 2100, calculated as the difference between currently similar regions and regions that are similar to the climate projected to occur in the Alps under future climate conditions. Areas that may emerge as new source areas are shown in red and areas in blue are those projected to become less suitable in the future.

Figure 4: Potential source areas under current and future climate conditions (Composite Match Index of 0.7 or greater) a) Regions of the world with climates currently similar to the Australian Alps Region b) Regions with current climates similar to the projected future Australian Alps climate c) Regions with future climates similar to that projected for the Australian Alps Region.

Figure 5: Ecoclimatic Index for *Hieracium aurantiacum* in the Australian Alps region for current and future (2080) climate conditions, based on three Global Climate Models under a high emissions scenario (RCP8.5).

Figure 6: Ecoclimatic Index for *Hieracium pilosella* and *Hieracium murorum* in the Australian Alps region for current and future (2080) climate conditions, based on three Global Climate Models under a high emissions scenario (RCP8.5).

Figure 7: Ecoclimatic Index for *Hieracium praealtum* in the Australian Alps region for current and future (2080) climate conditions, based on three Global Climate Models under a high emissions scenario (RCP8.5).

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Figure 1

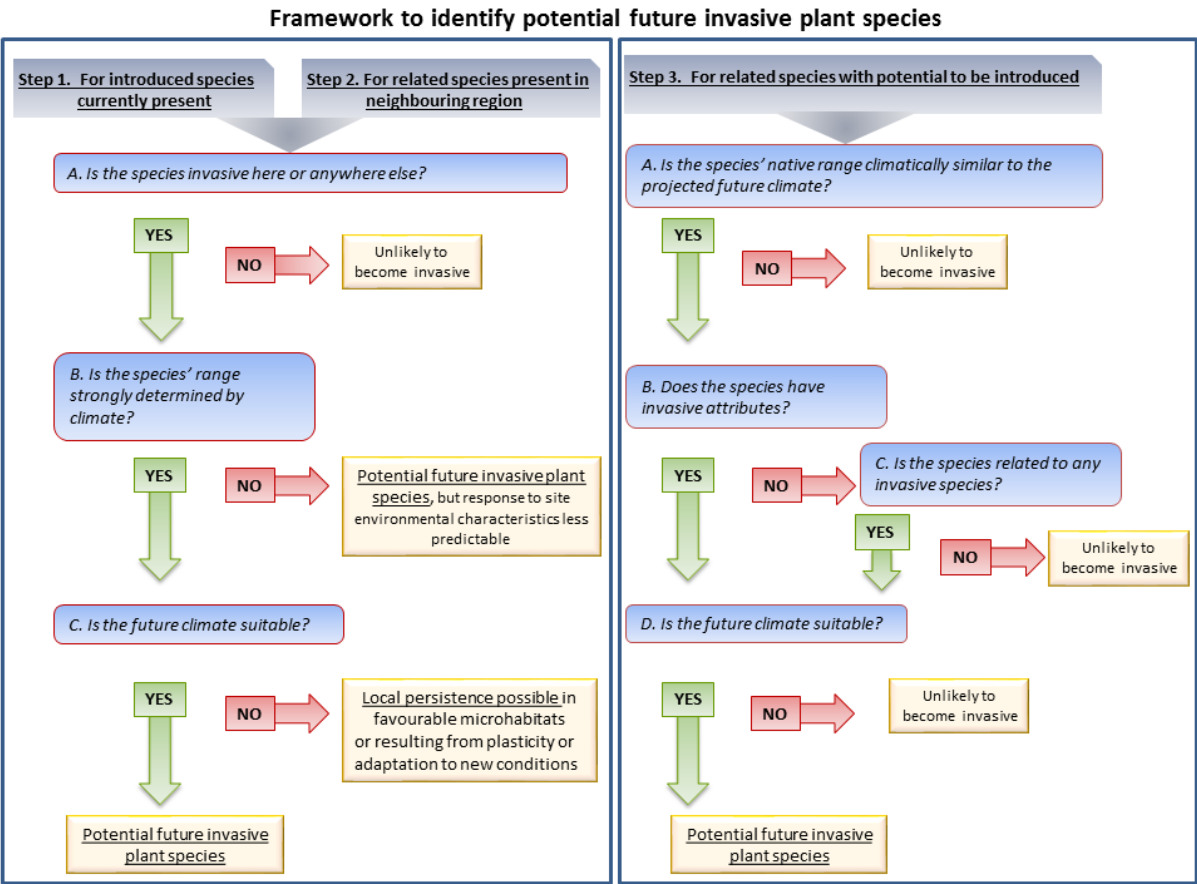


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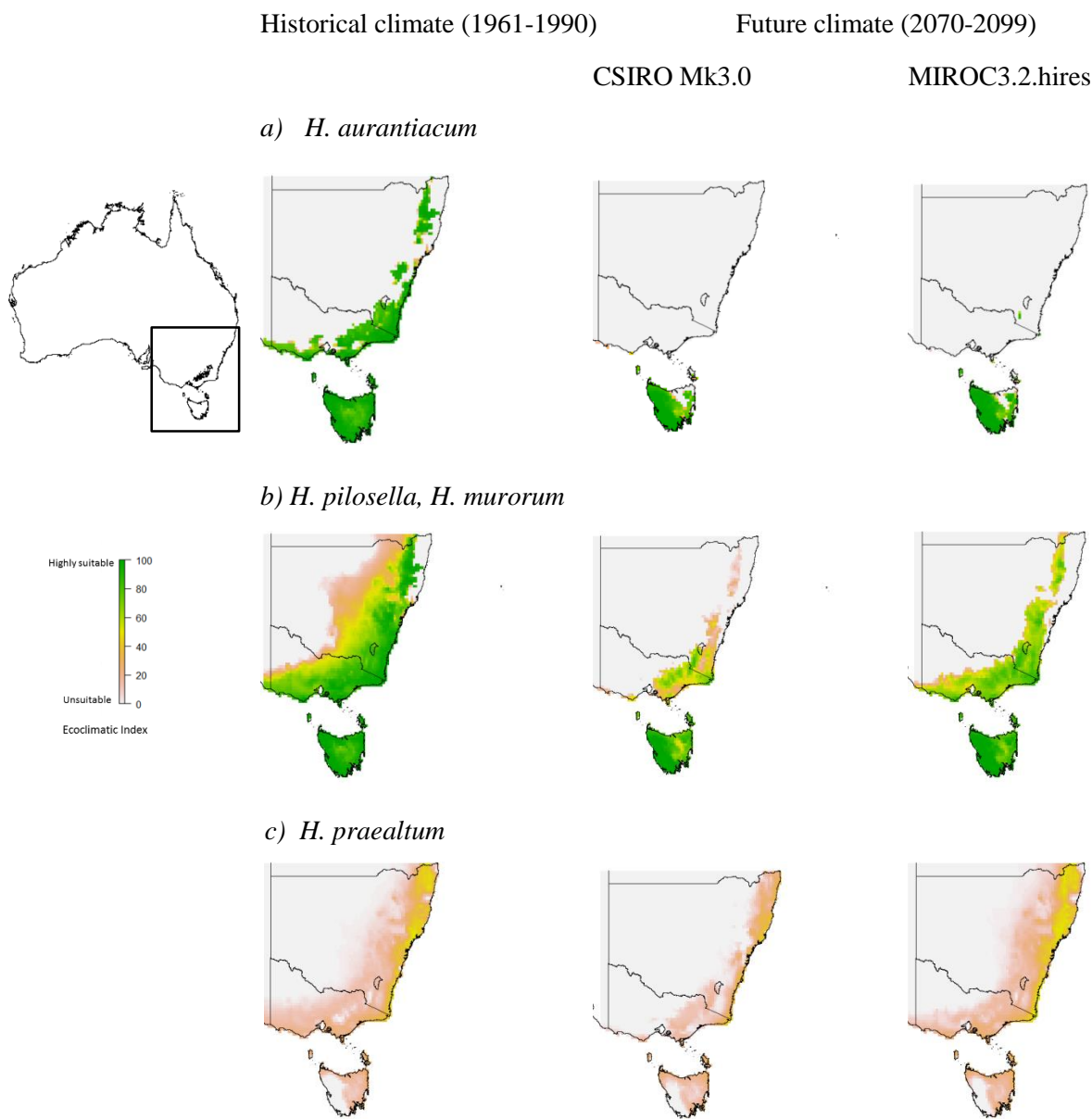
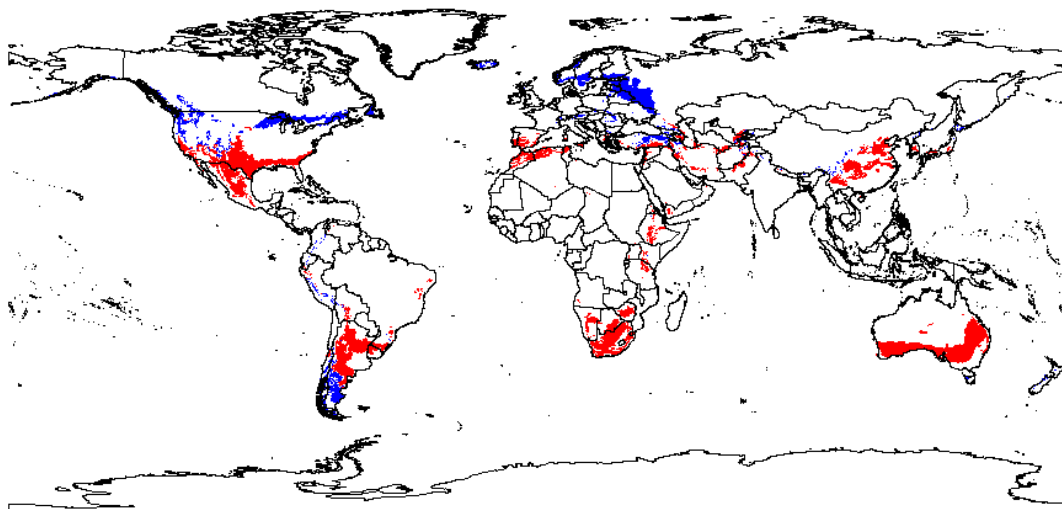


Figure 3

CSIRO Mk3.0



MIROC3.2.hires

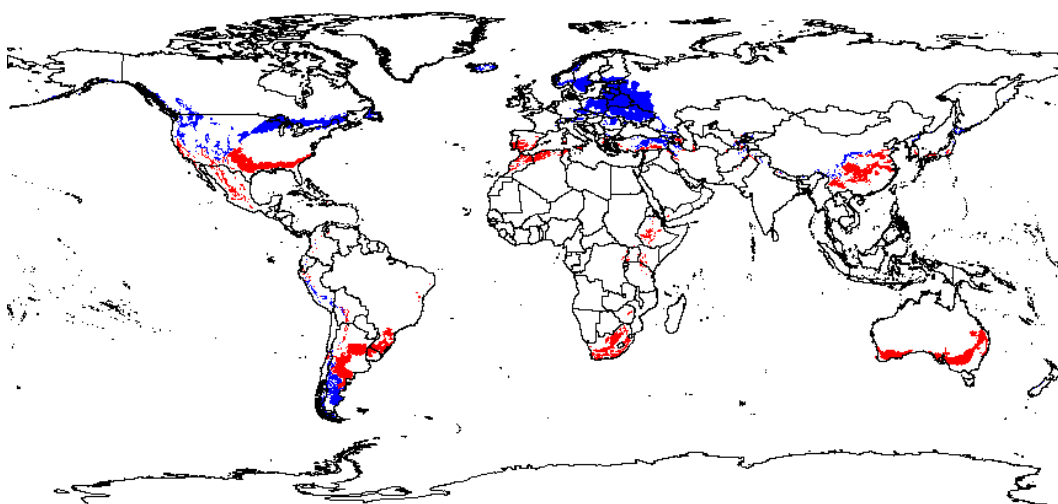
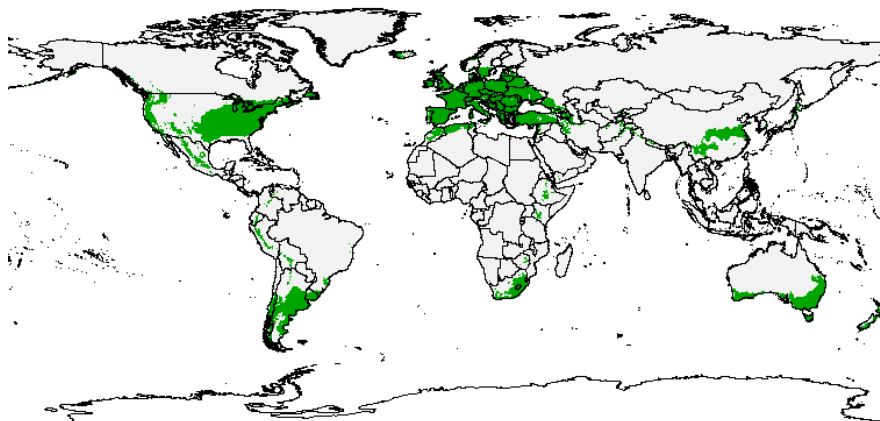
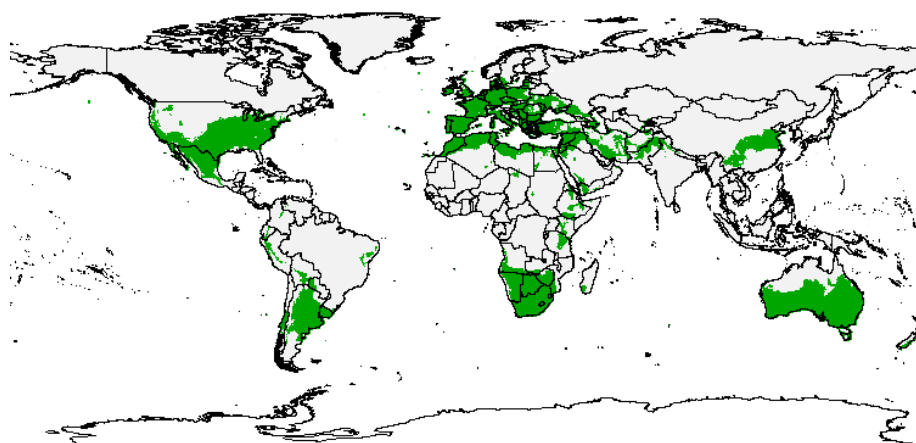


Figure 4

a)



b)



c)

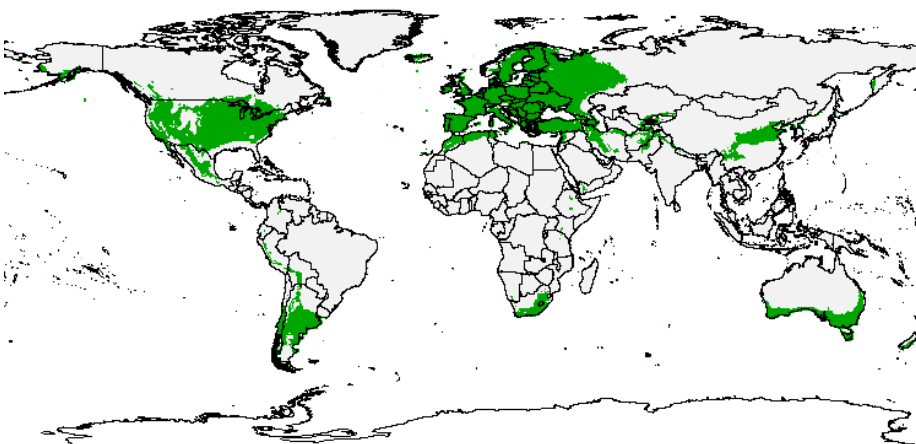


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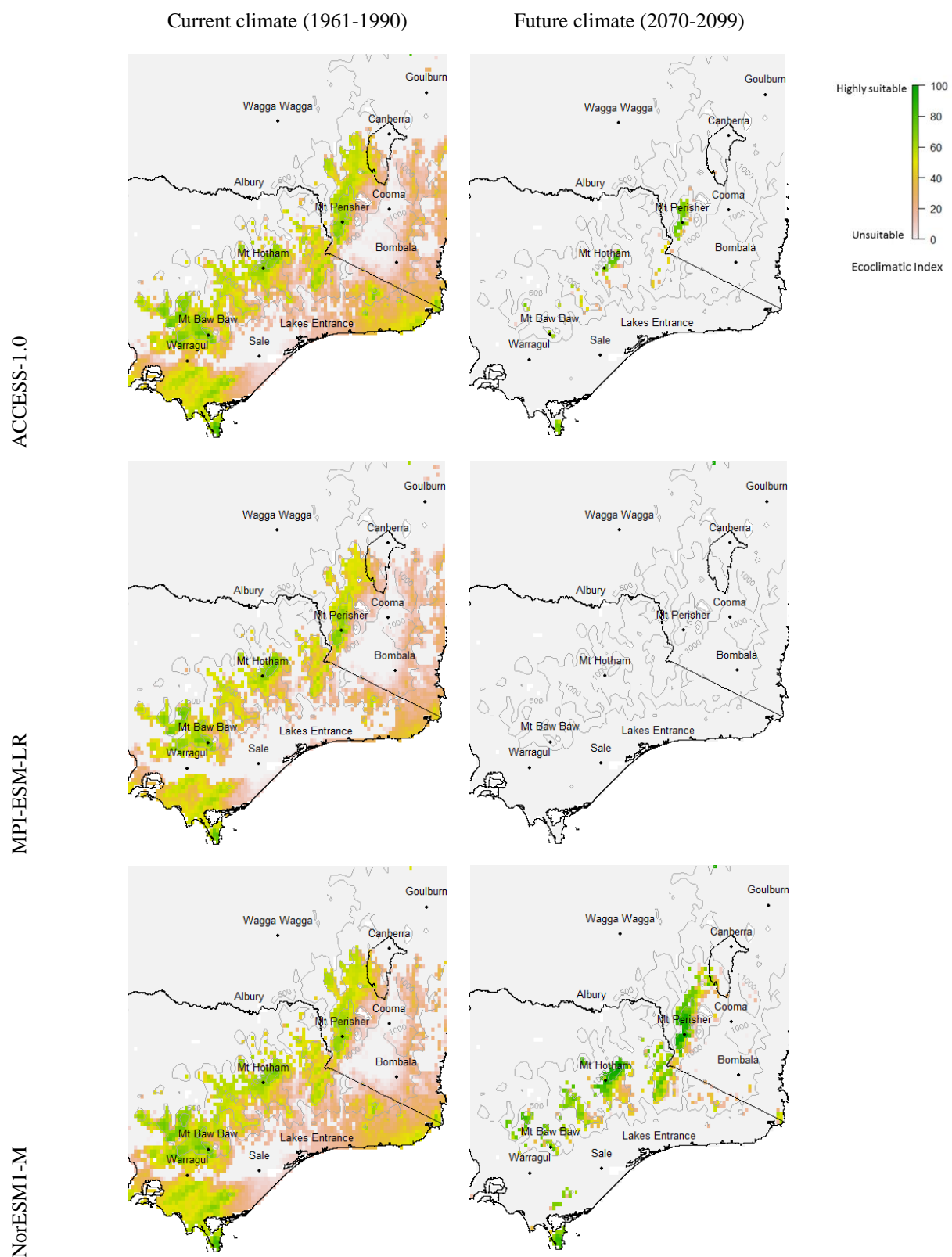


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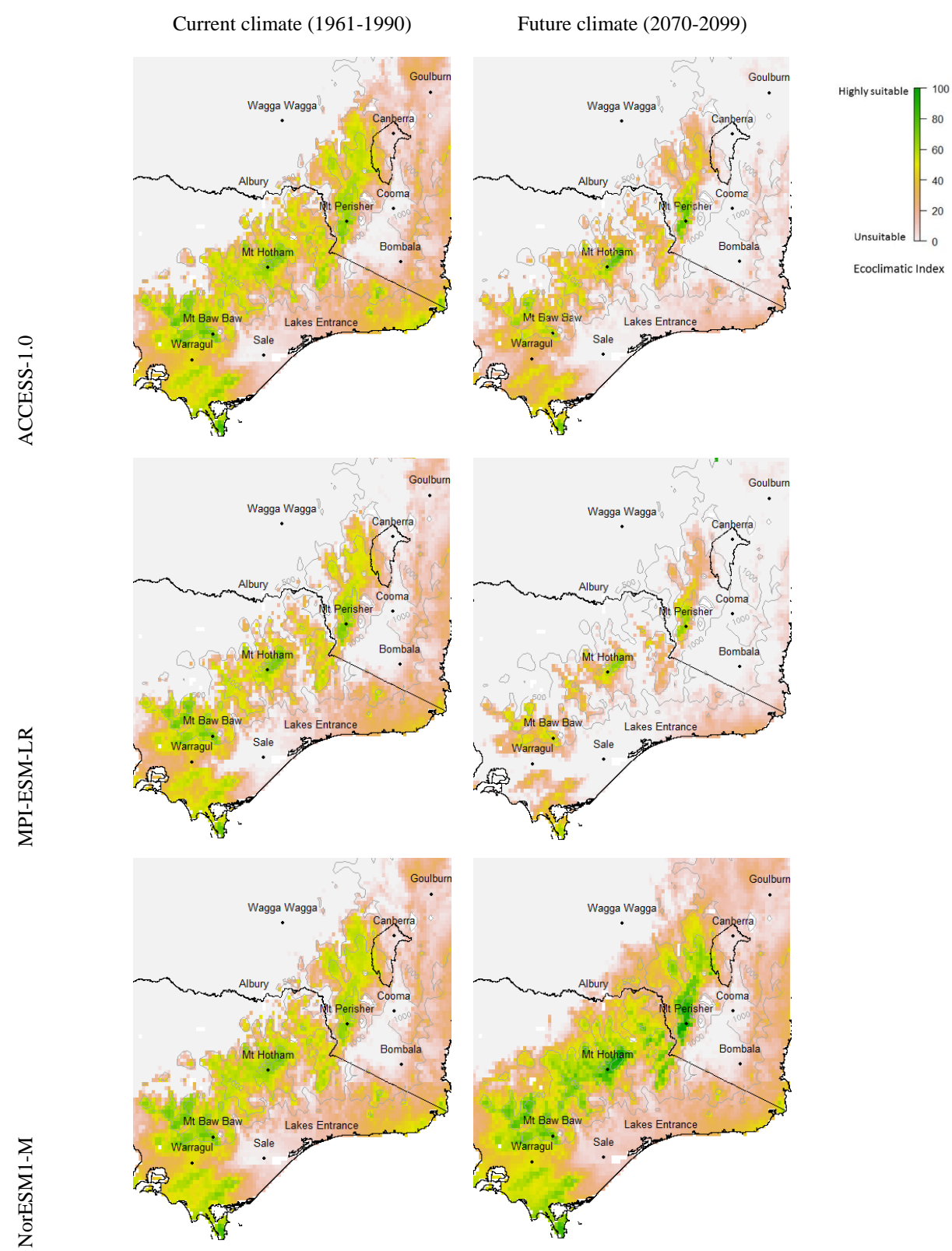
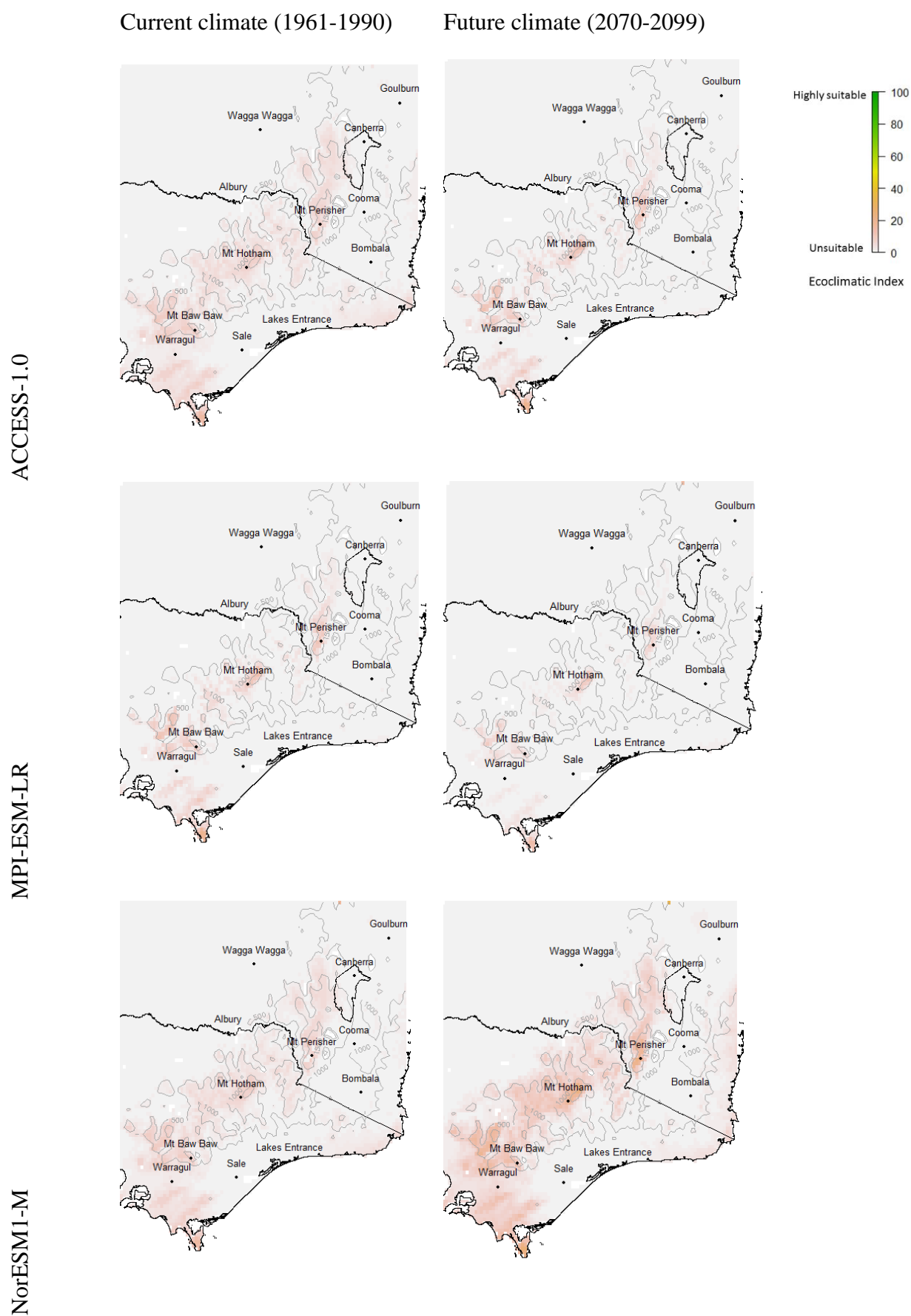
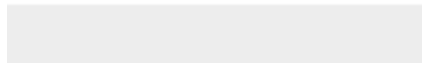


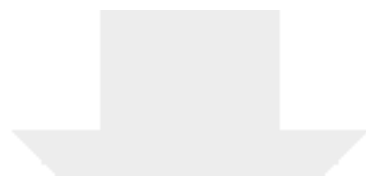
Figure 7



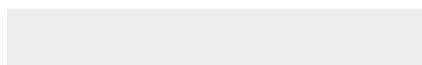
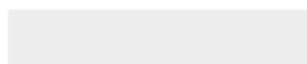


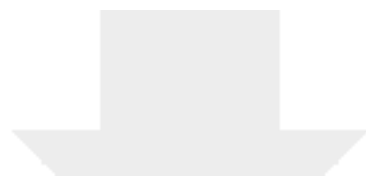
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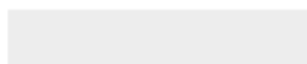


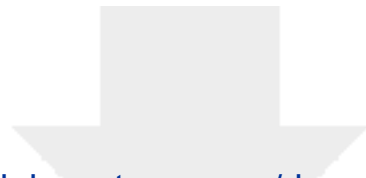
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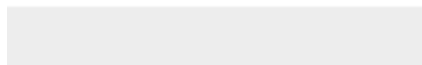


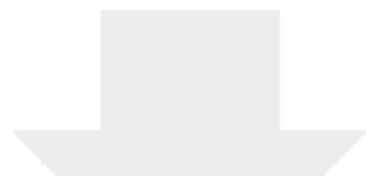
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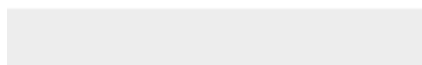
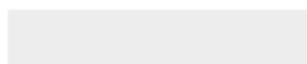


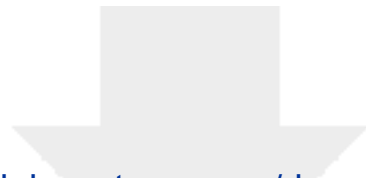
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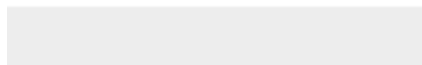
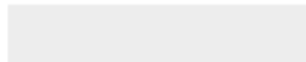


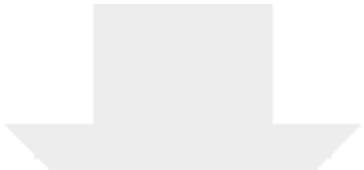
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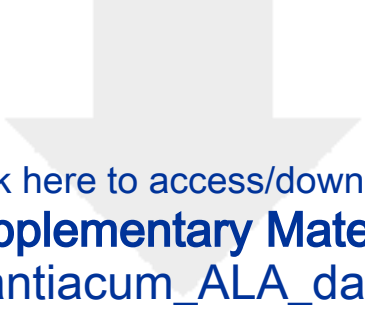
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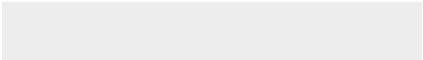



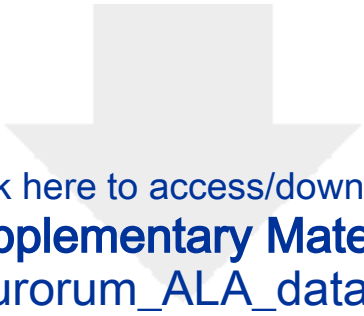
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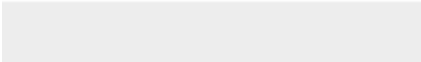



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