



The effect of climate change on crop wild relatives

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Abstract

Crop wild relatives are an important source of genetic diversity for crop improvement. However, the survival of some of these wild plant species could be threatened because of climate change. We used current and projected future climate data for ~2055, and a climate envelope species distribution model to predict the impact of climate change on the wild relatives of peanut (*Arachis*), potato (*Solanum*) and cowpea (*Vigna*). We considered three migrational scenarios for modeling the range shifts (unlimited, limited, and no migration). Climate change strongly affected all taxa, with an estimated 16–22% (depending on migration scenario) of these species predicted to go extinct and most species losing over 50% of their range size. Moreover, for many species, the suitable areas become highly fragmented. *Arachis* were the most affected group, with 24–31 (depending on the migration scenario) of 51 species projected to go extinct and their distribution area on average reduced by 85–94%, depending on the migration scenario, over the next 50 years. The number of patches was predicted to decrease by 19% under the no migration scenario or increase by 4% assuming unlimited migration. Patch size decreased by 55–60%. For *Solanum*, 7 (no migration) to 13 (unlimited migration) of 108 species were predicted to go extinct, and their range sizes were reduced by approximately 38–69%. The number of patches was predicted to decrease by 34% (no migration) or increase 7% (unlimited migration) and patch size decreased by 20 (unlimited migration) to 37% (no migration). In terms of species extinction, *Vigna* was the least affected of the three groups, losing no species (unlimited migration) to 2 species (no migration) of the 48 species in the genus. The mean range size was predicted to decrease by 65% (no migration) or increase 8% (unlimited migration), with 8–41 of the 48 species losing more than 50% of their current geographic range. The number of *Vigna* patches increased by 12–115%, but the size of those patches shrunk by 51–59%. Our results suggest that there is an urgent need to identify and effectively conserve crop wild relatives that are at risk from climate change. While increased habitat conservation will be important to conserve most species, those that are predicted to undergo strong range size reductions should be a priority for collection and inclusion in genebanks.

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1. Introduction

Crop wild relatives (CWR) include crop ancestors as well as other more or less closely related species. In the process of domestication, a crop goes through a genetic bottleneck, ending up with much less genetic variation than is available in the wild species. This genetic uniformity can make crops more vulnerable to biotic and abiotic stresses. CWR have been used in formal crop improvement programs for over 100 years

(e.g. Mujeeb-Kazi and Kimber, 1985; Large, 1940), especially for increasing resistance to insect pests and diseases. For example, they have been used to enhance resistance against wheat curl mite (Malik et al., 2003), late blight in potato (Pavek and Corsini, 2001), and grassy stunt disease in rice (Brar and Khush, 1997). Crop wild relatives are being used to improve tolerance of stressful abiotic conditions such as tolerance to drought in wheat (Faroq and Azam, 2001) and have been tested for heat tolerance in rice (Sheehy et al., 2005). They have also been used to raise the nutritional value of some crops, such as protein content in durum wheat (Kovacs et al., 1998), calcium content in potato (Bamberg and Hanneman, 2003), and provitamin A in tomato (Pan et al.,

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2000). It is expected that the use of CWR in breeding will increase due to recent advances in molecular technologies that increase efficiency and accuracy in transferring desired traits from CWR to crops (Hajjar and Hodgkin, 2007).

Seeds of many CWR have been collected and conserved in genebanks (*ex situ* conservation). This has greatly facilitated their use, but the world's genebanks are conserving only a fraction of the total genetic variability that exists in CWR and only a small proportion of conserved accessions have been characterized. Moreover, genebank collections are not exposed to natural selection processes that affect natural populations. Conservation of species *in situ* allows new variation to arise and species to adapt to gradual changes in environmental conditions and biotic interactions. This has been referred to as the conservation of the evolutionary process in addition to the current pattern of biodiversity (Pressey et al., 2003). Therefore, an *in situ* conservation approach is needed, complemented by the *ex situ* collections, to maintain a much larger reservoir of genetic diversity, and to ensure that habitats where CWR occur are protected and wild species continue to evolve in the wild.

Climate is one of the major factors governing the distribution of wild plant species, acting directly through physiological constraints on growth and reproduction or indirectly through ecological factors such as competition for resources (Shao and Halpin, 1995). The relatively modest climatic changes over the past century have had significant impacts on the distribution, abundance, phenology and physiology of a wide range of species. Many instances have been recorded of species range shifts towards the poles or upward in altitude, and progressively earlier seasonal migrations and breeding (e.g. Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006). Global warming has accelerated over the past 30 years (Osborn and Briffa, 2005), and is predicted to be in the range of 1.1–6.4 °C by 2100 (IPCC, 2007). Modeling studies (e.g. Thomas et al., 2004) indicate that climate change may lead to large scale extinctions.

Given the potential impact of climatic change on global food production (Rosenzweig and Parry, 1994; Hijmans, 2003; Jones and Thornton, 2003), and the demonstrated importance of crop wild relatives in breeding of novel varieties with improved adaptations to biotic and abiotic stresses, it is of paramount importance that crop wild relatives are adequately conserved. Safeguarding and using CWR to broaden the genetic base of modern crops is vital for adapting agricultural systems to the impacts and consequences of climate change (Sheehy et al., 2005). Yet due to climate change, these very genetic resources may themselves be under threat of extinction in the wild. Therefore, assessing the potential impact of climate change on CWRs and developing adequate conservation responses is a key activity to sustain agricultural production.

Climate envelope models provide a way to assess the likely impacts of climate change on wild species by predicting range shifts. Climate envelope models use

environmental data for the locations where a species has been found (or not found) to infer its climatic requirements. These inferred requirements can then be used to classify the suitability of any other location (Guisan and Thuiller, 2005).

A number of studies have applied climate envelope-based species distribution models to the problem of understanding the impacts of climatic change through the use of climatic data for the present and the future (Thomas et al., 2004) and the past (Ruegg et al., 2006). These methods essentially transfer a species adaptation temporally, assuming on the one hand no more plasticity than currently observed and on the other hand zero evolution, and many overlook the possible consequence of changes in biotic interactions such as competition (Lawler et al., 2006). There is a growing body of research evaluating the suitability of applying species distribution models to predicting range shifts and assessing extinction risk in the face of climate change (Thuiller et al., 2004; Araújo et al., 2005a,b; Araújo and Rahbek, 2006; Hijmans and Graham, 2006; Lawler et al., 2006).

A central question in the application of species distribution models to understanding the impacts of climate change relates to the migrational (dispersal) capacities of species (Pearson, 2006). Species capable of migrating at high rates are more likely to survive, and indeed in some cases may gain geographic range due to greater land mass in higher latitudes, and species–energy relationships (Menendez et al., 2006). Most modeling studies account for migration by assuming it to be either unlimited or non-existent, yet the reality is likely to be somewhere in-between (Pearson, 2006). Thomas et al. (2004) estimated extinction for a sample of species from various parts of the world under these two migrational scenarios, reporting extinction rates of 21–23% with unlimited migration, and 38–52% with no migration. When the migrational rate is known for a particular species, it is relatively easy to account for this in modeling (Midgley et al., 2006).

Despite the uncertainties associated with species distribution modeling applied to understanding the likely impact of climate change in species survival, the results are of importance because they can help select and prioritize actions to mitigate negative impacts. In this paper we use climate envelope models to assess the potential geographic shifts in distribution of wild species of three cultivated crops. Using three migrational scenarios, we evaluate changes in potential range size, and in fragmentation of these climatically suitable areas.

2. Materials and methods

2.1. CWR occurrence data

We selected the CWR of peanut (*Arachis hypogaea* L.), potato (*Solanum tuberosum* L.) and on African wild *Vigna* spp. which are related to cowpea (*Vigna unguiculata* (L.) Walp.) and Bambara groundnut (*Vigna subterranea* (L.)

Verdc.). These three taxa were selected as previous studies had already collated extensive georeferenced datasets of herbarium and genebank occurrence records (“point localities”) for biogeographic analyses; because they represented complementary geographic and environmental ranges (mountains and lowland savannahs in Latin America for potato and peanut respectively, and much of Africa in the case of *Vigna*); and because they are related to globally important crops.

There are 68 species of wild peanut (Krapovickas and Gregory, 1994), which occur in South America (Bolivia, Brazil, Paraguay, Argentina and Uruguay). The 187 species of wild potatoes occur from the southwestern United States through the highlands of Central and South America into Argentina, Chile, and Uruguay (Hijmans and Spooner, 2001; Spooner et al., 2004). In this analysis we only included *Vigna* species occurring in sub-Saharan Africa, comprising 61 species (Maxted et al., 2004). These species occur in a wide range of habitats but especially in grasslands, savannas, open woodlands and shrublands and generally at low to mid–low altitudes (Maxted et al., 2004).

Only species for which we had at least 10 distinct localities of occurrence were included in the analysis, resulting in a study of 210 individual species in the three groups analysed. Hernandez et al. (2006) who report a 30% prediction success using Bioclim with 10 samples. This increases to over 80% when 75 samples are used, but this threshold would have limited this study to just 61 species of the 316 species in the three genera. The small sample size used on 66 species (with 10–25 unique localities) is a potentially important source of error and should be considered when interpreting the results.

The wild peanut data (Jarvis et al., 2003) consisted of 2175 unique localities (here defined as unique species by locality combinations) for the 68 species but only 51 species had 10 or more unique localities. The wild *Vigna* data consisted of 7733 unique localities for 65 species (Maxted et al., 2004). Just 51 species had 10 or more localities, and were included in the species distribution analysis. The wild potato data (*Solanum* sect. *Petota*) consisted of 9822 unique localities for 187 species (Hijmans and Spooner, 2001; Spooner et al., 2004). Of these, 108 species had 10 or more localities and were used in the modeling.

2.2. Species distribution modeling

Many different statistical techniques have been used in species distribution modeling (Segurado and Araújo, 2004; Elith et al., 2006). We used the Bioclim model (Busby, 1991) as implemented in DIVA-GIS (www.diva-gis.org). While this model performed relatively poorly in the comparative study of Elith et al. (2006), we use it because it does not create response curves that may cause erratic behaviour when applied to new climates (Hijmans and Graham, 2006). While it is somewhat biased towards underestimating future species ranges, this study is largely comparative between

species and genera, and we assume that the method is valid provided the results about the absolute percentages of range change are interpreted with care. It is also easy and fast to run, both important considerations when dealing with as many species as we did. The semi-continuous output from the Bioclim model was transformed into presence/absence by assigning presence to the areas where the Bioclim scores were within the 2.5–97.5 percentile range. This threshold was applied for both current and future conditions, as is common practice (Hijmans and Graham, 2006). Because Bioclim may underestimate future ranges, an alternative approach would have been to use more relaxed threshold for future conditions (e.g. 0–100 percentile).

We ran this model to predict the current and future geographic distribution of each wild relative species under study. The environmental data consisted of climate surfaces for present and projected future conditions. For present climate we used WorldClim climate surfaces (Hijmans et al., 2005) because of their high spatial resolution (~1 km) and global extent. Future climate data are available from a number of global climate models (GCMs) with differing greenhouse gas emission scenarios, model characteristics and spatial resolutions. There is uncertainty in GCM predictions and the emission scenarios that drive them and the approach taken in many studies is to use several GCMs and emission scenarios (Stainforth et al., 2005). We did not consider variation between GCM projections due to time and processing constraints, although comparison between models and scenarios should be considered in future analyses. We used data from Govindasamy et al. (2003) because it had the highest spatial resolution available. They used the CCM3 model at a 50 km spatial resolution and for a concentration of CO₂ in the atmosphere of 600 ppm (two times that of pre-industrial conditions). This CO₂ concentration (including other greenhouse gasses expressed as CO₂ equivalents in terms of their warming potential) might occur around 2055. In order to match the 1 km resolution of the current climate conditions, a downscaling procedure was applied to the CCM3 data by calculating the predicted change in monthly means from the CCM3 model. These change data were then downscaled to 1 km resolution using smoothing (spatial interpolation), and added to the current WorldClim climatic surfaces.

For both present and future monthly climate data, the following ‘bioclimatic’ variables were derived: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter. Using this high number of variables, rather than a smaller subset, might in some cases lead to underestimation of predicted future range

Table 1

Average effect of climate change on potential distribution (climatically suitable area) of species from three crop wild relative genera^a

	<i>Arachis</i> (51 species)			<i>Solanum</i> (108 species)			<i>Vigna</i> (51 species)		
	Unlimited migration	Limited migration	No migration	Unlimited migration	Limited migration	No migration	Unlimited migration	Limited migration	No migration
Average area loss (%)	85	89	94	38	52	69	–8	51	65
No. of species with area gains	1	0	0	21	9	0	19	1	0
No. of species with area losses	26	51	51	79	92	95	31	50	48
No. of species with area loss = 100%	24	27	31	7	7	13	1	0	3
No. of species with area loss > 75%	41	42	47	23	37	48	3	6	13
No. of species with area loss > 50%	46	48	51	41	52	80	8	23	41

^a Data were averaged for each genus and computed for three migratory scenarios: unlimited, limited, and no migration (see Section 2).

sizes (Hijmans and Graham, 2006), but we did not investigate that here.

2.3. Range metrics for quantifying threat

We used the estimated current and future species ranges to calculate a number of range metrics that describe the extent and configuration of a species' range, that were subsequently used to calculate extinction risk. The range metrics were designed to capture three scenarios of migrational capacity, ranging from "unlimited" (populations can move to any site where the climate is suitable), to "limited" (populations can move a defined distance), to "no migration" (populations cannot move). 300 km was used as the migrational limit under the limited migration scenario, assuming that for most species this is a attainable distance of migration over a period of 50 years.

All range area metrics are analysed using Arc/Info and using Arc Macro Language (AML) scripts for automatization of the analysis. In addition to range area metrics, we calculated two metrics associated with the configuration of species distributions, with emphasis on fragmentation. For this, Patch Analyst V extension to Arcview 3.2 was used (<http://flash.lakeheadu.ca/~rrempel/patch/overview.htm>). The metrics calculated are total number of patches and average area of each patch for each of the three migrational scenarios.

2.4. Species richness

We mapped species richness under current and future conditions for each of the three taxa under the unlimited migration scenario and the no migration scenario in order to identify the broad spatial patterns of the impact of climate change. Broad patterns were analysed to examine shifts in species richness across latitudinal and elevational gradients.

3. Results

3.1. Climatically suitable area

For all migrational scenarios considered *Arachis* species were most affected, followed by *Solanum*, with *Vigna*

projected to be least affected (Table 1). The results here are presented in ranges derived from Table 1 covering the three migration scenarios. Climate change reduced the size of the climatically suitable area of 80–100% of species, affecting 98–100% of the *Arachis* species, 80–100% of the *Solanum* species, and 63–100% of the *Vigna* species. 16–22% of all species modeled were predicted to go extinct due to complete loss of climatically suitable areas. *Arachis* was most affected with 24–31 species (47–61% of species) facing extinction; *Solanum* sect. *Petota* was projected to lose 7–13 species (7–12% of species) and *Vigna* 0–2 species (0–8% of species).

Under the limited migration scenario, for *Arachis* species the average climatically suitable area was reduced by 89%, with 48 species losing more than 50%. Species with smaller climatically suitable areas under current climate tended to lose the greatest climatically suitable area in the future ($r^2 = 0.73$, $P < 0.001$). For *Solanum* species, loss of climatically suitable area averaged 52% with 52 species losing more than 50%. The relationship between the current climatically suitable area and future area loss was not significant ($r^2 = 0.07$, $P > 0.05$). *Vigna* species lost an average 51% of climatically suitable area and 23 species suffered losses of over 50%. As found for *Solanum*, the relationship between current climatically suitable area and future area loss was not significant ($r^2 = 0.19$, $P > 0.05$) for *Vigna*.

The effects of climate change were much larger under the no migration scenario. Obviously no species saw gains in climatically suitable area as species could not move into new areas. Complete loss of climatically suitable areas (i.e. extinction) was projected for 31 *Arachis* species, 13 *Solanum* species and 3 *Vigna* species.

In order to aid in the prioritization of species targeting for conservation, a list of priority species based on extinction probability, percentage loss of climatically suitable area and projected future range size is presented in Table 2. The projected average future climatically suitable area for *Arachis* species was 36,486–74,867 km² but 1–3 species on top of the 24–31 predicted to lose all area will have climatically suitable areas of less than 500 km² (including *A. batizocoi*, *A. gracilis* and *A. kempff-mercadoi*). For *Solanum*, the average future climatically suitable area is 38,672–

Table 2

List of priority species for conservation based on likelihood of extinction, percentage loss of range size and predicted remaining range area, assuming unlimited dispersal

	Predicted extinction (no future range area)	10 species with <10,000 km ² future range area (km ²)	10 species with greatest % loss of range area (% loss)
<i>Arachis</i>	<i>A. appressipila</i> , <i>A. archeri</i> , <i>A. benensis</i> , <i>A. cryptopotamica</i> , <i>A. douradensis</i> , <i>A. guaranitica</i> , <i>A. hatschbachii</i> , <i>A. helodes</i> , <i>A. hermannii</i> , <i>A. lignosa</i> , <i>A. marginata</i> , <i>A. palustris</i> , <i>A. setinervosa</i> , <i>A. simpsonii</i> , <i>A. stenophylla</i> , <i>A. magna</i> , <i>A. tuberosa</i> , <i>A. hoehnei</i> , <i>A. burkartii</i> , <i>A. retusa</i> , <i>A. glandulifera</i> , <i>A. paraguariensis</i> , <i>A. pseudovillosa</i> , <i>A. decora</i>	<i>A. benthamii</i> (9465), <i>A. cardenasii</i> (5163), <i>A. correntina</i> (3264), <i>A. triseminata</i> (1308), <i>A. matiensis</i> (802), <i>A. batizocoi</i> (717), <i>A. oteroi</i> (609), <i>A. subcoriacea</i> (301), <i>A. gracilis</i> (232)	<i>A. gracilis</i> (99%), <i>A. kretschmeri</i> (99%), <i>A. oteroi</i> (99%), <i>A. matiensis</i> (99%), <i>A. subcoriacea</i> (98%), <i>A. triseminata</i> (97%), <i>A. kempff-mercadoi</i> (96%), <i>A. major</i> (96%), <i>A. batizocoi</i> (96%), <i>A. correntina</i> (95%)
<i>Solanum</i>	<i>S. velardei</i> , <i>S. tarnii</i> , <i>S. xmichoacanum</i> , <i>S. xrechei</i> , <i>S. ugentii</i> , <i>S. chancayense</i> , <i>S. incamayoense</i>	<i>S. irosinum</i> (5), <i>S. paucissectum</i> (5), <i>S. hoopesii</i> (41), <i>S. piurae</i> (87), <i>S. raquialatum</i> (146), <i>S. longiconicum</i> (179), <i>S. arnezii</i> (193), <i>S. lignicaule</i> (250), <i>S. acroscopicum</i> (422), <i>S. xsambucinum</i> (475)	<i>S. irosinum</i> (99%), <i>S. hoopesii</i> (97%), <i>S. piurae</i> (96%), <i>S. xsambucinum</i> (96%), <i>S. paucissectum</i> (95%), <i>S. acroscopicum</i> (95%), <i>S. raquialatum</i> (93%), <i>S. jamesii</i> (91%), <i>S. arnezii</i> (88%), <i>S. trifidum</i> (85%)
<i>Vigna</i>	No species	<i>V. monantha</i> (16), <i>V. virescens</i> (38), <i>V. keraudrenii</i> (110), <i>V. phoenix</i> (363), <i>V. mungo</i> (1066), <i>V. richardsiae</i> (2866), <i>V. bosseri</i> (3686), <i>V. hosei</i> (4387), <i>V. mudenia</i> (9590)	<i>V. keraudrenii</i> (98%), <i>V. decipiens</i> (85%), <i>V. phoenix</i> (78%), <i>V. procera</i> (64%), <i>V. mungo</i> (63%), <i>V. angivensis</i> (59%), <i>V. antunesii</i> (56%), <i>V. gazensis</i> (55%), <i>V. platyloba</i> (51%), <i>V. juncea</i> (50%)

60,000 km² but 7–8 species are predicted to have climatically suitable area of less than 500 km². *Vigna* species had a relatively large future climatically suitable area of about 1.26–2.40 million km² and apart from the 0 to 2 species projected to go extinct (*V. longifolia* and *V. keraudrenii*), no species had less than 500 km² of climatically suitable area in the future. Species with a relatively small climatically suitable area are more vulnerable to loss of genetic diversity and possibly extinction and could be priority species for conservation actions. For peanuts, species with less than 1000 km² projected to be suitable in the future included: *A. batizocoi*, *A. burkartii*, *A. decora*, *A. glandulifera*, *A. gracilis*, *A. kempff-mercadoi*, *A. kretschmeri*, *A. matiensis*, *A. oteroi*, *A. paraguariensis*, *A. pseudovillosa*, *A. retusa*, and *A. subcoriacea*. For *Vigna* the suitable area for most species remains high, although specific habitat constraints may mean the actual distributional area is significantly less than reported with the climate suitability models. Only one species faced intermediate threat and that is *V. angivensis*, an endemic to Madagascar, with 26,000–61,000 km² of predicted future area (a loss of 71–82% of current climatically suitable area). For *Solanum*, species with less than 1000 km² of predicted future climatically suitable area were *S. arnezii*, *S. acroscopicum*, *S. clarum*, *S. lignicaule*, *S. limbanianense*, *S. piurae* and *S. raquialatum* and *S. xsambucinum*.

It is important to note that not all species had a reduction in their climatically suitable area under climate change. No *Arachis* species gained area, but some 19 *Vigna* species gained area under the unlimited migration scenario with *V. praecox* gaining as much as 4.1 times its current climatically

suitable area, and four other species (*V. longifolia*, *V. nyangensis*, *V. radiata*, *V. richardsiae*) more than doubling their climatically suitable area. Under limited migration only *V. schlechteri* gained climatically suitable area (0.42 times current area), and under no migration there were no gains. For *Solanum*, 21 species gained area assuming unlimited migration, and nine species under the limited migration scenario. However, only three species gained more than 10% of current area (*S. hastiforme*, *S. maglia* and *S. xsambucinum*) and none more than 30%.

A number of wild relatives of peanut that have been used in breeding are projected to lose a considerable amount of climatically suitable area: *A. diogoi* Hoehne (77–97% loss) and *A. batizocoi* Krapov. (96–98% loss) has provided resistance to root-knot nematode; *A. cardenasii* Krapov. (93–99% loss) for resistance to corn earworm and southern corn rootworm (Stalker and Lynch, 2002); and *A. paraguariensis* (100% loss) and *A. appressipila* (100% loss), have been used as a source of resistance to early leaf spot (ICRISAT, 1995).

Amongst *Solanum* species, *S. demissum*, which has resistance to late blight (Ross, 1986), kept 33–90% of the size of its currently suitable area; *S. chacoense* and *S. berthaultii* with resistance to Colorado potato beetle (Plaisted et al., 1992) will lose 40–53% and 2–65% of distribution areas, respectively; and *S. microdontum*, which can be used to breed for varieties with increased calcium content (Bamberg and Hanneman, 2003) stands to have a change of –28 to 9% in its suitable area.

A number of wild *Vigna* species that are sometimes collected and eaten by humans (Padulosi and Ng, 1990), and

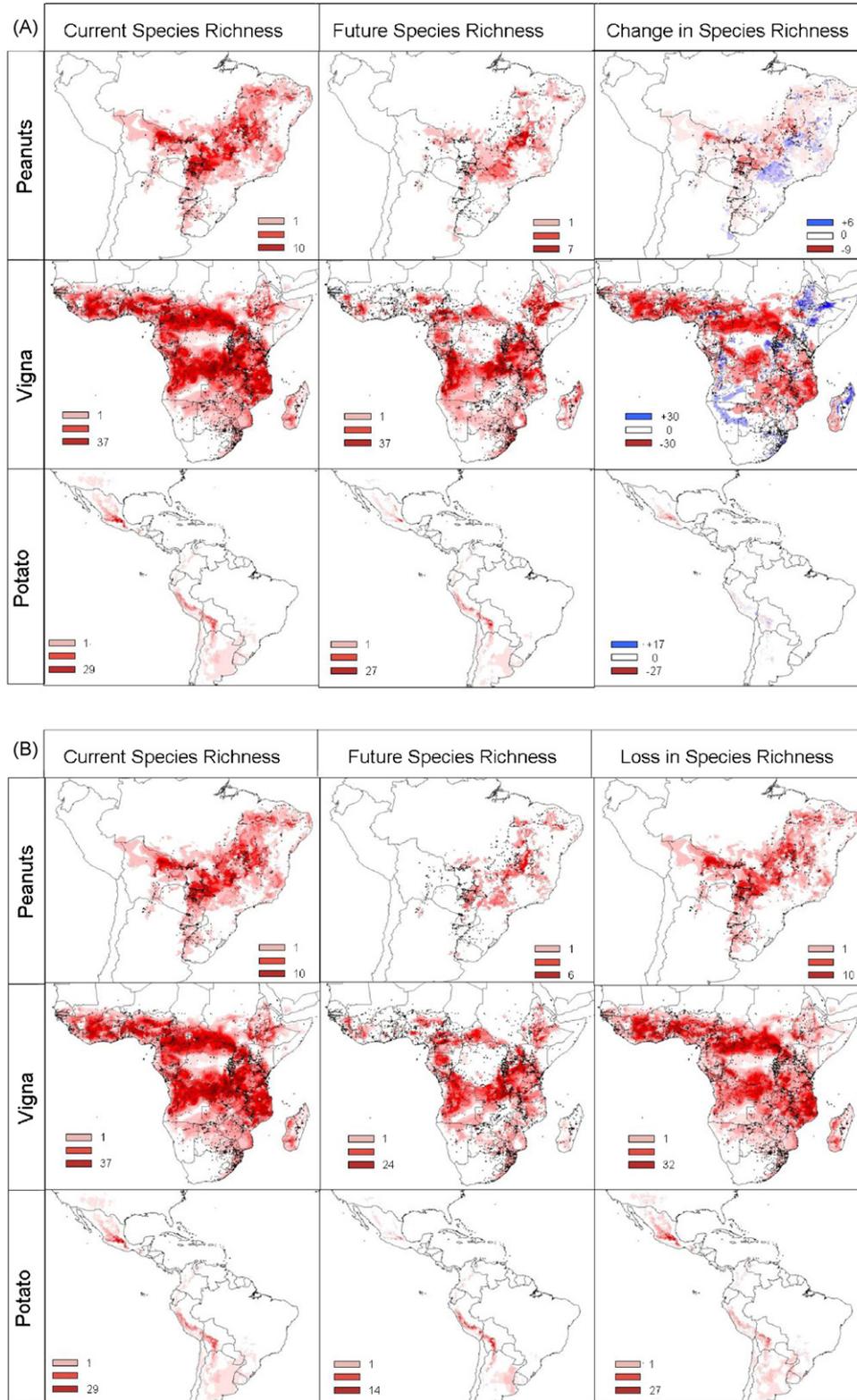


Fig. 1. Modeled potential species richness under current and future climate scenarios and the difference between the two for each of three groups of crop wild relative species. Peanuts (*Arachis*), potatoes (*Solanum*), and *Vigna* (related to cowpea and bambara groundnut) species (data shown are for (A) an unlimited migration scenario and (B) a no migration scenario).

thus contribute to food security, are under threat from climate change. For example, the tubers of *V. adenantha* (50–68% area loss) and the fruit and seeds of *V. junceum* (50–80% area loss) are eaten. *V. stenophylla*, a species of which the tubers are eaten, stands to gain 67% or lose 93% of area depending on the migrational scenario.

3.2. Species richness

The change in the patterns of species richness under the unlimited migration scenario (Fig. 1a) and no migration scenario (Fig. 1b) was variable in space and between the

three CWR groups. There is a general pattern of *Arachis* species moving south-eastwards towards some of the cooler climates of the higher elevations of south-east Brazil under the unlimited migration scenario. Species richness at lower latitudes was least affected, and the general trend of species richness across the elevational gradient shifts some 200 m upwards (Fig. 2). Indeed, species richness increased at 800–1100 m assuming unlimited migration. For *Solanum*, species richness diminished most in lower elevations as areas suitable for species moved upwards. Greatest losses in species richness were found in mid-northern latitudes (20–25°N) and far southern latitudes (20–40°S). Under the

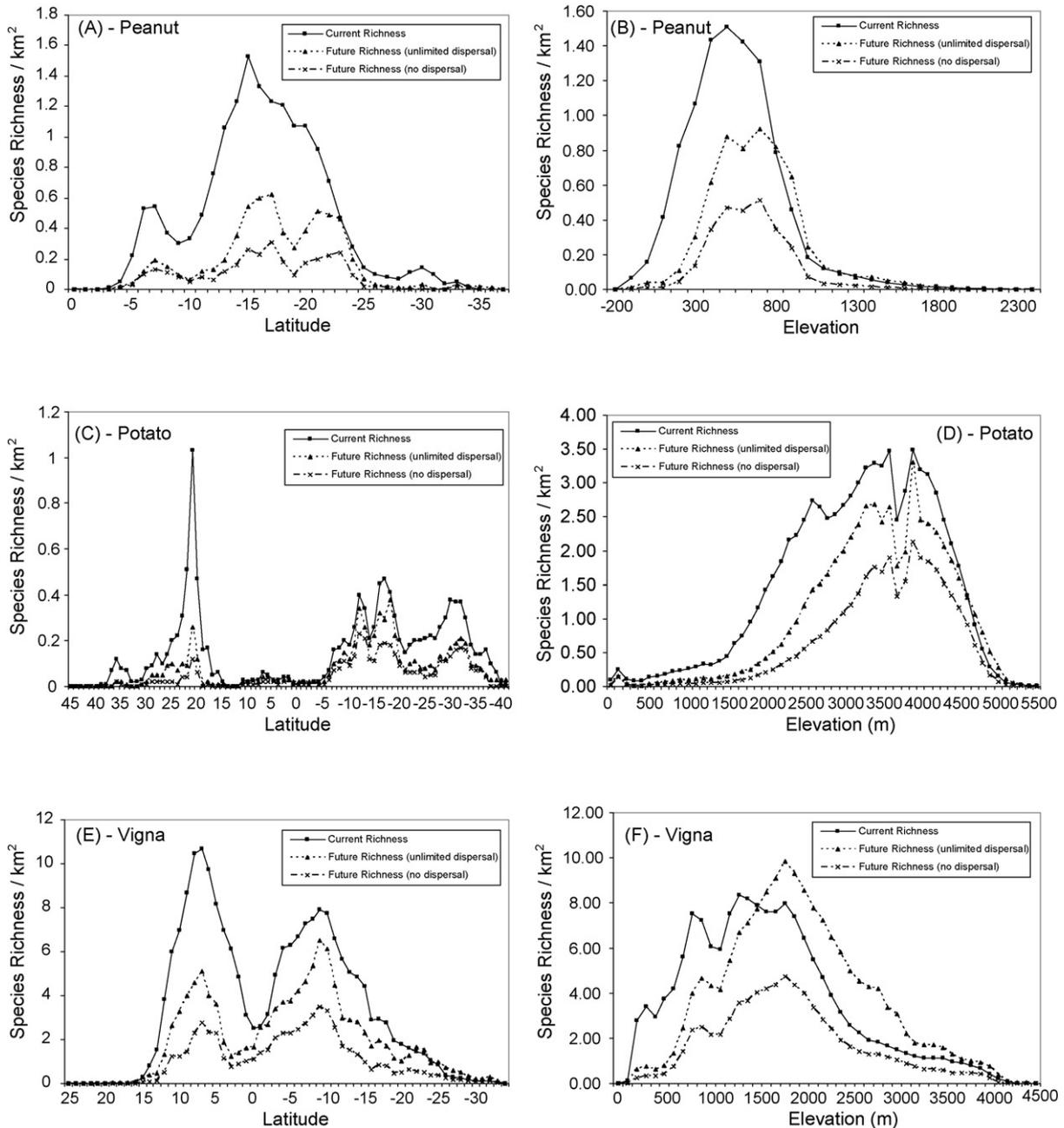


Fig. 2. Shifts in species richness across latitudinal and elevational gradients for each of three groups of crop wild relative species. A and B: *Arachis*; C and D: *Solanum*; E and F: *Vigna* species.

Table 3

Predicted effect of climate change on patch size and area for the potential distribution (climatically suitable areas) of species from three crop wild relative genera^a

	<i>Arachis</i> (51 species)			<i>Solanum</i> (108 species)			<i>Vigna</i> (51 species)		
	Unlimited migration	Limited migration	No migration	Unlimited migration	Limited migration	No migration	Unlimited migration	Limited migration	No migration
Current average patch area (km ²)		65			39			199	
Future average patch area (km ²)	26	29	27	28	32	25	84	98	81
Current number of patches		1538			1309			9461	
Future number of patches	1600	1246	1314	1397	858	891	20403	11143	10568

^a Data are averaged by genus and computed for three migratory scenarios: unlimited, limited, and no migration (see Section 2). The number of patches and average patch size in the future is calculated based only on species predicted to survive.

unlimited migration scenario, *Vigna* species moved southwards into South Africa and northwards particularly into Ethiopia. Greatest losses occurred in northern latitudes (0–15°N), and at low elevations. Under unlimited migration species richness increased at elevations above 1500 m.

3.3. Fragmentation of suitable area

Current habitat patches of *Arachis*, *Solanum* and *Vigna* became smaller as a result of climate change (Table 3). Again, *Arachis* species were most affected, with the average patch size decreasing by 55–60%. The total number of patches, however, remained relatively stable, with a 4% gain assuming unlimited migration, and a 19% loss under the no migration scenario. The smaller the habitat patch for these species under current conditions the greater the loss of area in the future ($r^2 = 0.42$). For *Solanum*, there was a 20–37% decrease in average patch size, accompanied by a 7% increase to 35% decrease in total number of patches. There was no relationship between current patch size and future loss of climatically suitable area ($r^2 < 0.001$). *Vigna* species gained 12–115% in the number of patches, but had decreases in average patch size of 51–59%.

Potentially most at risk from fragmentation were *Solanum* species as the patch sizes are in general low, both at present (39 km²) and in the future (25–32 km²). The number of patches for many *Vigna* species increased and for one to four species, which had some of the smallest mean patch sizes, patches actually increased in size under some or all migrational scenarios. These species were *V. schlechteri* (1–43% increase), *V. juncea* (13% increase to 28% decrease), *V. davyi* (5% increase to 40% decrease) and *V. procera* (7% increase to 14% decrease), the latter despite losing 64–72% of climatically suitable area. This species is restricted to southern-central-west Africa where it is uncommon (Maxted et al., 2004).

4. Discussion and conclusions

The results presented in this paper are based on inherently uncertain model predictions. Nevertheless, they do provide a strong indication that climate change alone presents a

significant threat to important agricultural genetic resources, specifically the wild relative species studied here, with 16–22% of species predicted to have no climatically suitable areas and perhaps go extinct by 2055. When climate change effects are combined with alteration of habitats and other anthropogenic impacts, the status of many of these species should be considered as highly threatened, and measures to conserve the genetic resources will need to be expanded.

The impacts of climate change on CWR were shown to be heterogeneous in space, and also variable depending on habitat and migrational capacities of the species under question. This is evident in the difference in predicted extinction rates between the three groups of CWR, with 47–61% of *Arachis* species facing extinction compared to just 2–6% of *Vigna* species predicted to be facing extinction. The high extinction rates in *Arachis* species may be due to their fairly narrow adaptation to hot and dry climates which become hotter and dryer in the future, confounded by the fact that they are found in flat regions meaning that large migration distances are needed for them to track their climatic bands. Potatoes on the other hand, despite being highly endemic, benefit from existing in places with significant environmental gradients, providing a diversity of niches and short migration distances to track their climate. *Vigna* species tend to be broadly adapted, and hence tend to lose only a limited portion of their climatically suitable area regardless of migration.

It is important to note that even within the CWR groups, significant differences in impacts were observed between species, implying that conservation planning in the context of climate change should occur at the species level.

4.1. Uncertainties in predictions

There are a number of sources of uncertainty about the projections presented here. One of the principal problems with the use of species distribution modeling is that when they are used to project future conditions, the results cannot be validated (Araújo and Rahbek, 2006). Some authors have used hindcasting to validate modeling approaches, whereby the past is used as a key to the future (Martínez-Meyer et al., 2004; Araújo et al., 2005a). Uncertainty due to differences between modeling algorithms and climate projections can be

addressed through multi-model inference (Guisan and Thuiller, 2005) and sensitivity analysis. However we considered that beyond the scope of this study given the large amount of species and large geographic areas covered. Rather we opted for a preliminary analysis to investigate whether we would find large responses and variation between species and groups of CWR.

Our results might overstate the threat from climate change to some species because Bioclim has been shown to underestimate distributional area with climate change and because we use many environmental variables (Hijmans and Graham, 2006). However, the analysis presented here also fails to account for other impacts on species distribution, like past, present and future habitat alteration and harvesting of species from the wild. This may lead to overestimation of future suitable area as species are already severely limited in distributional area and migrational capacity due to fragmentation of habitats. Climate models should ideally be coupled with land-use projection models to understand the current pattern of habitat fragmentation and predicted future patterns based on projection of parameters that drive land-use change such as population and consumption (Hannah et al., 2002). Another source of uncertainty is in the case of new climates, where climate change brings about climatic conditions not currently experienced. This occurs especially in hot lowland regions, where future temperature increases create climatic conditions with temperatures not currently found. This is the case in some regions where wild peanuts are currently found. Finally it is important to note that climate envelope models do not take into account competition, habitat or other biotic interactions, and the extent to which plasticity is accounted for is under debate (Parmesan, 2006). The model used here does not take into account these complex interactions, which will also be affected by climate change.

Another major source of uncertainty stems from assumptions made about plants' capacity to migrate, though it is known that many plant species have a low capacity to migrate (Pearson, 2006). We found considerable variability in the results depending on the migrational scenario used, especially for fragmentation measures. The significant differences in extinction rates between the groups studied are of interest. Essentially, for a species to maintain its range size in the face of climatic change the species must migrate at a rate equal or greater to the speed of horizontal displacement of climates, or be able to adapt to keep pace with a changing climate. The horizontal displacement of climate depends partly on the magnitude of the climate change in that particular region, and landscape characteristics such as topographic heterogeneity. Relatively flat areas are likely to have much faster horizontal displacements in climate than mountainous regions, where a climate could be tracked over short distances by moving uphill. Many *Arachis* spp. are predicted to suffer higher extinction rates due to their distribution in predominantly flat regions where the horizontal displacement of climate is fastest. Furthermore,

the fate of wild *Arachis* may be further compounded by a migrational capacity that has been reported to be as low as 1 m per year (Gregory et al., 1973), but no empirical data are available, and this rate seems very low given the large distribution areas of some species, and the fact that they have survived Pleistocene and earlier climate change that caused large range shifts for many species (Waltari et al., 2007).

4.2. Implications for conservation

The economic value of crop wild relatives to sustainable agriculture is large. The contributions of CWR to crop yield and quality of US-grown or US-imported crops were calculated to be over \$340 million a year in the early 1980 (Prescott-Allen and Prescott-Allen, 1983), and this figure is likely to have increased since then. Our study has shown that many crop wild relatives of *Arachis*, *Solanum* and *Vigna* that have already been important for crop-breeding programs are under threat from climate change. The importance of CWR genes to peanut breeding is clearly demonstrated by the fact that nearly half of new peanut cultivars and germplasm lines registered in Crop Science journal between 2000 and 2005 contained CWR in their pedigrees. Breeding for resistance and tolerance in crops is essential to continue adaptation of farming systems to changed and irregular climate conditions.

Strategically placed protected areas may be key in preserving genetic diversity (Lavendel, 2003). Areas selected should be evaluated for their potential as climate change refugia for vulnerable species. Such reserves should contain target populations large enough to ensure persistence as the larger the number of individuals of a species in a given area, the greater the probability that the species will survive (Araújo et al., 2004). For *in situ* conservation of species like *Arachis* that are highly vulnerable to climate change impacts and with a limited capacity to migrate and with little time to adapt may require human intervention such as translocations.

Some crop wild relatives, including some *Solanum* and *Vigna* species are weedy or early colonizers and prefer disturbed environments. Thus, these species do not require pristine habitat and persist along roadsides provided that disturbances are not too frequent or intense. Road networks and other tracts of disturbed areas could become corridors for the migration of these species (Peters et al., 2005). However, for species requiring pristine habitat, fragmentation creates spatial barriers to species migration and diminishes colonisation of suitable habitats. Prevention and reduction of habitat fragmentation therefore is critical to mitigating impacts of climate change (Lavendel, 2003). Migration corridors to connect landscape fragments could facilitate range shifts of mobile species. Linking corridors between habitat patches expand the potential range of species and, as indicated by this study for some groups, larger areas have greater buffering potential against climate change than smaller areas.

The analyses presented here can be a starting point in prioritizing species for conservation in the wild (*in situ*). However, our results are most relevant for *ex situ* conservation approaches in which seeds are stored in genebanks. Climate change must be a fundamental consideration in conservation management, and selection of new protected areas and management plans for existing areas need to account for its projected impacts.

4.3. Future work

Further investigation is needed in order to better understand the potential impacts of climate change on plant species in the wild. Firstly, different climate envelope models should be used and the results analysed to examine agreement between models. Different GCM models and scenarios should also be used to further identify where agreement in model results converges or diverges. These measures could contribute to estimating, and perhaps reducing, the uncertainty in the results.

Secondly, experimental studies could contribute to a better understanding of the true adaptation of wild species to changing climates. *Arachis* species, for example, are currently found in some of the hottest and driest parts of Latin America. Climate change is expected to create new climates not currently found on the continent. The degree to which these species adapt to these new very high temperatures is not known and could be examined through experimental work similar to that proposed by Zavaleta (2006). Experimental studies could take advantage of *ex situ* collections and perform common-garden experiments of populations in different climatic environments (representing present and future climates) in order to gain a mechanistic understanding of the physiological basis of climatic adaptations.

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