Developing methodologies for the global *in situ* conservation of crop wild relatives

By

Holly A. Vincent

A thesis submitted to the University of Birmingham for the degree of

DOCTOR OF PHILOSOPHY

School of Biosciences

The University of Birmingham

June 2016

ABSTRACT

Climate change is predicted to have far-reaching deleterious impacts worldwide; agriculture in particular is expected to be effected by significant loss of suitable land and crop yields in the world's most populous and poorest regions. Crop wild relatives (CWR) are a rich source of underutilised genetic diversity which could help to mitigate climate change for agriculture through breeding new resilient varieties. However, CWR are under-conserved and threatened in the wild. This thesis researches and develops systematic methodologies to advance knowledge and support action on *in situ* CWR conservation at the global level. Methods included developing a global inventory of CWR associated with crops important for food security worldwide, species distribution modelling, climate change analysis, *in situ* gap analysis, reserve planning and prioritisation, and, examining the congruence of CWR distributions with regions of high biodiversity and crop diversity. The methods described here can be applied to CWR at both the national and regional level to ensure robust *in situ* CWR conservation. A principal success of this research is the global CWR inventory, which has been used in several national strategies and as the basis of a major *ex situ* germplasm collection mission worldwide.

“Only if we understand can we care. Only if we care will we help. Only if we help shall they be saved”

Jane Goodall

“Do. Or do not. There is no try”

Yoda, The Empire Strikes Back

DECLARATION

The work presented in Chapter 2 and Appendix 1has been published and Chapters 3–5 are being prepared for publication. The wording of Chapter 2 and Appendix 1 is largely identical to the manuscripts prepared for publication. All chapters were written by me and represent my own work.

Chapter 2:

Vincent, H., Wiersema, J., Kell, S., Fielder, H., Dobbie, S., Castañeda-Álvarez, N.P., Guarino, L., Eastwood, R., León, B. and Maxted, N. (2013) A prioritised crop wild relative inventory to help underpin global food security. *Biological Conservation* 167: 265–275.

Appendix 1:

Vincent, H., Castañeda-Álvarez, N.P., Maxted, N. (2016) An approach for *in situ* gap analysis and conservation planning on a global scale. In: Maxted, N., Ehsan Dulloo, M. and Ford-Lloyd, B.V. (eds.) *Enhancing Crop Genepool Use: Capturing Wild Relative and Landrace Diversity for Crop Improvement*. CAB International, Wallingford, UK. ISBN-13: 978-1-78064-613-8.

Signed:

HollyVincent
Student

Supervisor

27/06/2016
Date

ACKNOWLEDGEMENTS

I would like to thank my supervisor Nigel Maxted for his guidance and support throughout a challenging project. I would also like to thank John Wiersema for donating his knowledge and time to help me in the creation of the Harlan and de Wet Inventory. Thanks to Tamara Smekalova, Natalia, Galina and Mikhail for their help in photographing and translating Russian herbarium material and for making me feel so welcome in Russia.

I would also undoubtedly have lost hope and my mind without the support and friendship of my colleagues from S208. So, thank you to the whole CWR team, in particular, Hannah Fielder, Laura Rhodes and Jade Phillips for listening and for the games of Dobble. Particular thanks to Hannah for her support during write-up and encouraging me to keep going and not give up completely.

I could not have carried out this work without funding from the Global Crop Diversity Trust and support from the University of Birmingham. I am also grateful to the European PGR Secure project for invitations to various conferences; I learned a great deal and met some wonderful people.

I would finally like to thank my family, partner and friends for their tireless encouragement and emotional support. In particular, my parents for always encouraging me and helping wherever they can.

TABLE OF CONTENTS

LIST OF FIGURES

Figure A1.2 Top 50 complementary sites from the ‘all priority CWR’ best solution.

LIST OF TABLES

LIST OF SUPPLEMENTARY TABLES (on CD)

Supplementary Table 2.1 Global priority CWR list with numbers of *ex situ* collections (data sourced from GBIF), arranged by crop.

Supplementary Table 2.2 Number of CWR per country. TG = Taxon group concept, GP = Gene pool concept, PGP = Provisional gene pool concept.

Supplementary Table 2.3 CWR in the primary gene pool with fewer than 50 *ex situ* accessions recorded in GBIF (2013).

Supplementary Table 3.1 Bioclimatic, edaphic and geophysical variables used for species distribution modelling

Supplementary Table 3.2 *In situ* gap analysis results per CWR

CHAPTER 1

Introduction

1.1 Life on Earth

The Earth is a constantly evolving and interlinked system where every living organism depends on others for their survival. Together, all of these living organisms constitute the World's total biodiversity. An oft cited and widely accepted definition of biodiversity is *"…the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*" (UNCED, 1992). This is a wide definition including diversity on many scales from biological domains and kingdoms down to the species, population and the individual level with the alleles contained therein.

It is estimated that Earth's biodiversity currently encompasses 8.7 million eukaryotic species, including 7.8 million animal species, 298,000 plants species and 611,000 species of fungi (Mora *et al*., 2011). Using these estimates, only 14% of land based species are currently described with even fewer sea species described at 9%. New species are continuously being discovered and described, for example, between 2009 and 2014, over 200 new species were discovered in the Eastern Himalaya region alone (WWF, 2015), including three wild banana species: *Musa markkui* Gogoi & Borah, *Musa puspanjaliae* Gogoi & Häkkinen and *Musa kamengensis* Gogoi & Häkkinen.

Biodiversity, in the taxonomic sense of species and taxa, is not equally distributed across the globe; instead it is found concentrated in key areas (Gaston, 2000; Myers *et al*., 2000). In particular, Gaston (2000) remarks that many of the highly biodiverse areas are found near the equator, likely due to favourable climate and high rates of primary production. However, little is known about the distribution of genetic diversity within taxa and populations, and whether it similarly follows a heterogeneous pattern of geographic distribution (Gaston, 2000).

Life on Earth is currently endangered; it is estimated that up to two thirds of terrestrial species could become extinct by the end of this century (Millennium Ecosystem Assessment, 2005). Humans have had an impact on every habitat on Earth and are widely believed to be the driving force behind the ongoing global decline of biodiversity (Hoekstra *et al*., 2010; Pimm *et al*., 1995, 2014; Ceballos *et al*., 2015)

1.2 Biodiversity and human influence

1.2.1 The biodiversity crisis

Humans are an extremely successful and versatile species. In the short time frame since evolving some 200,000 years ago, they have developed medicine, created a plethora of technology, completely transformed natural habitats to their needs and increased their population size dramatically. Despite these successes, the extreme growth of the human population has also given rise to the current biodiversity crisis, with rates of habitat, biota and genetic diversity loss at an exceptionally high level (Butchart *et al.*, 2010). In fact, it is widely agreed that we are living in the age of Earth's sixth great extinction, with rates of species loss 100 times greater than the background level, outpacing those of pre-human times and previous mass extinctions (Ceballos *et al*., 2015; McCallum, 2015). In terms of species loss, Fischlin *et al.* (2007) report that by 2100, 10-30% of species globally could be at high risk of extinction, similarly, the 2015 IUCN Red List assessed the extinction risk of 4% of the World's described species and has found a third of the currently assessed species are threatened with extinction (IUCN, 2015). The Millennium Ecosystem Assessment (2005) reports a more drastic estimate with up to two thirds of terrestrial species becoming extinct by the end of the century. Furthermore, there is also a huge erosion of genetic diversity underway, which is more difficult to monitor and quantify in relation to population and individual losses of species, due to its unseen nature (Millennium Ecosystem Assessment, 2005). Maxted *et al.* (1997a) add that the loss of genetic diversity within populations will always be at a greater rate than the loss of species rate.

The human drivers of biodiversity loss are numerous but stem from two major demands, the demand for food and the demand for energy, which, in turn, lead to other drivers of loss as shown in Figure 1.1.

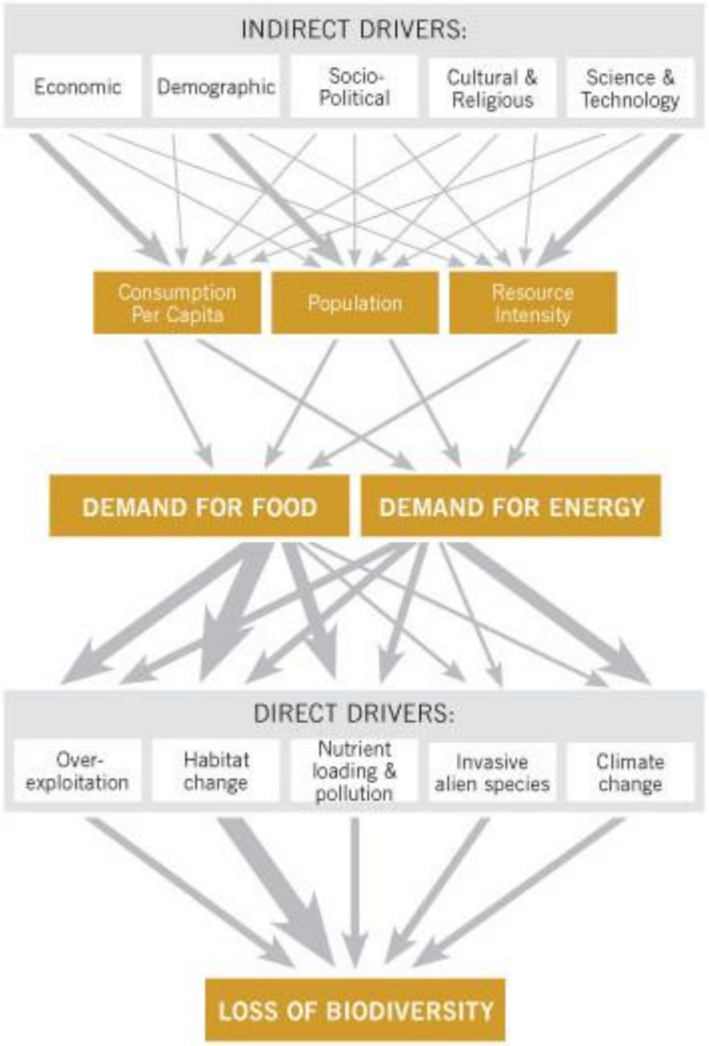

Figure 1.1 Drivers of biodiversity loss, extracted from Secretariat of the Convention on Biological Diversity (2006). Width of arrows indicates an approximation of the importance of the factor in driving biodiversity loss.

One of the greatest indirect drivers of biodiversity loss is the demand for energy, which has soared since the inception of the industrial era and the rise of capitalism and vast consumerism globally. The exploration for, and extraction of, oil and natural gas to meet energy demands is often extremely damaging to ecosystems, with major water pollution, destruction of natural habitats and endangerment of indigenous communities as by-products of the process (Finer *et al.*, 2009). Unfortunately, areas rich in oil and natural gas are often found in highly biodiverse regions, such as the Amazonian regions of Ecuador and Peru. The burning of fossil fuels was the main contributor (78%) to the increase in greenhouse gases from 1970 to 2010, and is the major causative factor to human induced climate change, which is expected to have an immense deleterious effect on biodiversity (IPCC, 2014). Additionally, greenhouse gases from agriculture, fisheries and forestry sectors has increased 100% in the last 50 years, with agriculture being the largest contributor (Tubiello *et al.*, 2014) and could continue to grow 30% up to 2050. In fact, emissions from agriculture have increased over 14% in the last 10 years alone (Tubiello *et al.*, 2014).

Stocker *et al.* (2013) suggest that human induced climate change has been the main cause of increases in global mean temperatures and also increased occurrences of extreme weather events since mid-century. Furthermore, they predict that climate change will increase the global mean surface temperature by 0.3– 0.7 °C by 2035 and significantly alter patterns in precipitation, with more intense rain in tropical forests and monsoon regions. Additional abiotic effects of climate change are expected to include: increased heatwaves, storms and fires, whilst weather patterns in general are to become more unpredictable (Sutton *et al.*, 2013); a rise in current sea levels due to increased temperatures melting glaciers (Arendt *et al.*, 2002; Church *et al.*, 2006); and ocean acidification caused by increases in CO_2 concentration (Hoegh-Guldberg and Bruno, 2010). Some examples of biotic effects are: coral bleaching (Wellington *et al.*, 2001), an increase and geographical shift in plant pests and diseases (Bebber *et al.*, 2013), and fragmentation and potential loss of habitat for important plants (Jarvis *et al.*, 2008).

The global demand for food also exerts a great negative pressure on biodiversity. Demand for food is currently being satisfied in many countries by expanding agricultural land coverage via large scale destruction of natural ecosystems and biodiversity; for example, large scale clearing of the Amazon rainforest for cattle farming and cash crop agriculture (Foley *et al.*, 2007; Gibbs *et al.*, 2015) and Indonesian forest clearing and burning for palm oil cultivation (Wicke *et al.*, 2011). However, irreversible habitat change is only one part of the current biodiversity crisis, with increasing demand for food also encouraging over-exploitation of natural resources (Scanlon *et al.*, 2007; FAO Fisheries and Aquaculture Department, 2012) and pollution of terrestrial habitats and water systems via harmful agricultural methods (Scanlon *et al.*, 2007; Geiger *et al.*, 2010; Potts *et al.*, 2010) which lead to further biodiversity depletion. Agriculture is not the only driver for habitat destruction, further influences stem from: expansion of human settlements; tourism; mining for precious metals (Swenson *et al.*, 2011; Edwards *et al.*, 2013) and exploitation of natural energy reserves (Finer *et al.*, 2009) to name but a few.

Biodiversity and the availability of the ecosystem services it provides are closely interlinked and necessary for human well-being, security and ultimately, survival (Millennium Ecosystem Assessment, 2005; Diaz *et al.*, 2006; Bauch *et al.,* 2015; Cardinale, 2012). As recent studies have shown that biodiversity loss causes changes in ecosystem processes (Hooper *et al.*, 2012; Mace *et al.*, 2015; Maseyk *et al.*, 2016), it is vital that the human race acts now to stem the loss of biodiversity, at the genetic, population and taxonomic level and reduce negative impacts on the environment, for our species’ future security.

1.2.2 Agriculture and the race for food security

The dawn of agriculture began roughly 10,000 years ago and has since contributed significantly to human diets. The FAO (2016) estimate that throughout the developing world there are currently 500 million smallholder farmers supporting the dietary requirements of nearly 2 billion people. In Asia and Sub-Saharan Africa, regions where malnourishment is extremely high, smallholder farmers produce roughly 80% of the food consumed there. During recent decades there has been a move away from traditional farming practices which grow locally adapted crop genetic diversity to high yielding varieties. This so called 'green revolution' caused the abandonment and permanent loss of thousands of locally adapted, genetically diverse crop varieties known as landraces (Ford-Lloyd *et al.*, 2011). However, these high yielding varieties are genetically poor in comparison to landraces, having gone through a severe domestication bottleneck and lack the genetic diversity to cope with pest and disease attacks leaving them vulnerable (Tanksley and McCouch, 1997; van de Wouw *et al.*, 2009) and requiring large quantities of pesticides and resource inputs to remain productive. Furthermore, Khoury *et al.* (2014) reports that diets globally are becoming increasingly homogenous, with reliance on fewer crops and varieties, leading to increased vulnerability of our food security.

Reliance on crops with a narrow genetic base, particularly in a monoculture system, can leave farmers and wider consumers vulnerable to severely reduced harvests and even famine if aggressive pest or disease outbreaks attack certain varieties (Esquinas-Alcázar, 2005). For example, the Irish potato famine was caused by over-reliance on monoculture agriculture and, in particular, a variety of potato called the 'Irish Lumper'. As potatoes propagate vegetatively, all of the crop grown were clones and genetically uniform. The variety was extremely vulnerable to the HERB-1 strain of the oomycete *Phytophthora infestans* which spread across the Americas to Europe, causing late blight in potato crops. At the time the 'Irish Lumper' potato fed roughly 40% of the total Irish population, whilst also providing a great significant amount of fodder for cattle. In 1845 potato crops were severely decimated by this pathogen reducing crop yield to 50–75% of normal with following years reducing crops by three quarters. This reliance on genetically non-diverse crops over a large geographical area led to one million deaths from starvation and malnutrition (Fraser, 2007).

Food security can be defined as "A situation that exists when all people, at all times, have physical, social and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life" (FAO, IFAD and WFP, 2015). Currently 1 in 9 people worldwide is suffering from chronic hunger (FAO, IFAD and WFP, 2015) and, with the human population estimated to increase to 9.6 billion by 2050 (UN, 2014), the number of people suffering from hunger is likely to increase. South Asia is the region most affected with 281 million people undernourished, followed by Sub-Saharan Africa with 220 million undernourished (FAO, IFAD and WFP, 2015). Projections for 2050 show that Africa is expected to have a population increase of 1.3 billion, whilst Asia is expected to gain an additional 0.9 billion people (UN, 2015). Food insecurity is not restricted to developing countries; for example, in the UK between 2014 and 2015 1,084,604 people, including 396,997 children, were provided with three days' worth of emergency food supplies, with low income and loss/problems with state benefit payments reported as the main drivers behind reduced access to adequate food supplies (The Trussell Trust, 2015). Food insecurity similarly affects some parts of society in the USA, with a reported 6.9 million households in the USA having suffered very low food security at some point in 2014 and a further 10.5 million households were in low food security (Coleman-Jensen *et al.*, 2015). To feed a global population of over 9 billion in 2050, it is estimated that food supplies will need to increase by 70–100% from current levels (Godfray *et al.*, 2010); however this prospect may be further dampened by the increasing effects of climate change. Multiple studies on the effects of climate change on agriculture have conclusively highlighted negative outcomes in terms of crop yield losses and loss of suitable agricultural land (Lobell *et al.*, 2008; Jarvis *et al.*, 2012; Challinor *et al.*, 2016). Jarvis *et al.* (2012) used climatic modelling to assess the future climate suitability for major food staples grown in Africa; they found that beans were projected to lose 16% of their current cropping area and potato was expected to lose 14.7%, however cassava was expected to be positively impacted by climate change. Porter *et al.* (2014) suggests that there could be 2% crop yield losses per decade up to 2050 due to the impacts of climate change, with increasing losses beyond mid-century. In addition to the direct threats climatic change is predicted to have on crops and food security, it is also likely to cause a rise in threat from crop pests and diseases (Bebber *et al.*, 2013; Uleberg *et al.*, 2014). To combat these pressing issues, Challinor *et al.* (2016) state that we must begin to adapt our agriculture now, as the time taken between introgressing beneficial traits with crops and the crops finding their way to the farmers field can take up to 30 years.

The compounding issues of unprecedented biodiversity loss, unsustainable agriculture, current and future food insecurity and climate change highlights the need for more efficient agricultural systems to feed the World, especially under a changing climate. This thesis focuses on these core themes and works towards developing strategies to improve food security via crop breeding and preventing biodiversity loss via conservation.

1.3 Plant genetic resources: the key to food security

Plant genetic resources (PGR) are a subset of biodiversity and provisioning ecosystem service, particularly useful to human agriculture and crop breeding (Millennium Ecosystem Assessment, 2005). Hawkes *et al.* (2000) categorise PGR, in particular those for food and agriculture, into several groups including: landraces, crop wild relatives (CWR), cultivars, weed races and breeding lines. Landraces and other cultivated material have long been the favoured sources of traits for crop improvement due to the ease of gene transmission and reduced linkage drag in comparison to wild material (Evenson and Gollin, 2001). Linkage drag is the process in which unwanted genes and traits are carried over to offspring from parents crossing along with the desired trait, so further breeding is needed to eliminate these side effects. In spite of crop improvements gained from landraces and breeding lines, Ford-Lloyd *et al.* (2011) state that the genes required to produce climate resilient crop varieties are likely to come from species that occupy more inhospitable and marginal habitats, in particular CWR.

1.3.1 Crop wild relatives

CWR are the wild and weedy relations of crops, including progenitors, which can be used as a source of novel genes and traits in plant breeding. CWR have been successfully utilised in crop breeding for decades; most notably in improving crop quality and resistance to pests and disease (Hajjar & Hodgkin 2007). A CWR can be simply defined as "… any plant taxon belonging to the same genus as a crop…" (Maxted *et al.*, 2006), however, this definition can lead to a very large number of CWR taxa where many are cross incompatible with the related crop and difficult or currently impossible to utilise in plant breeding (for example, the majority of *Glycine* Willd. species are cross incompatible with soybean using existing breeding methods). Using this broad definition, Kell *et al.* (2008) found that three quarters of the total Euro-Mediterranean flora (over 20,000 species) can be considered CWR. Furthermore, Maxted and Kell (2009) estimated that globally there were greater than 50,000 CWR using this method. Effectively conserving this number of CWR *in situ* and *ex situ* is not economically viable, particularly for long term actions. A more precise method of targeting and prioritising CWR for conservation is required to efficiently conserve these taxa. Harlan and de Wet (1971) proposed one such method of prioritisation; the gene pool (GP) classification of crops and their wild relatives, in which CWR species can be classified into differing levels of relatedness to the crop depending on how successfully the two hybridise (Figure 1.2). GP1A contains the cultivated taxa, whilst GP1B lists all closely related taxa that easily hybridise with the crop, often including progenitors and con-specific wild types. GP2 contains more remote taxa that can hybridise to produce partially fertile offspring, but more effort is often required to successfully transfer target traits to offspring without linkage drag. Finally, GP3 contains taxa where gene transfer is currently impossible or requires advanced techniques including use of other species as bridges.

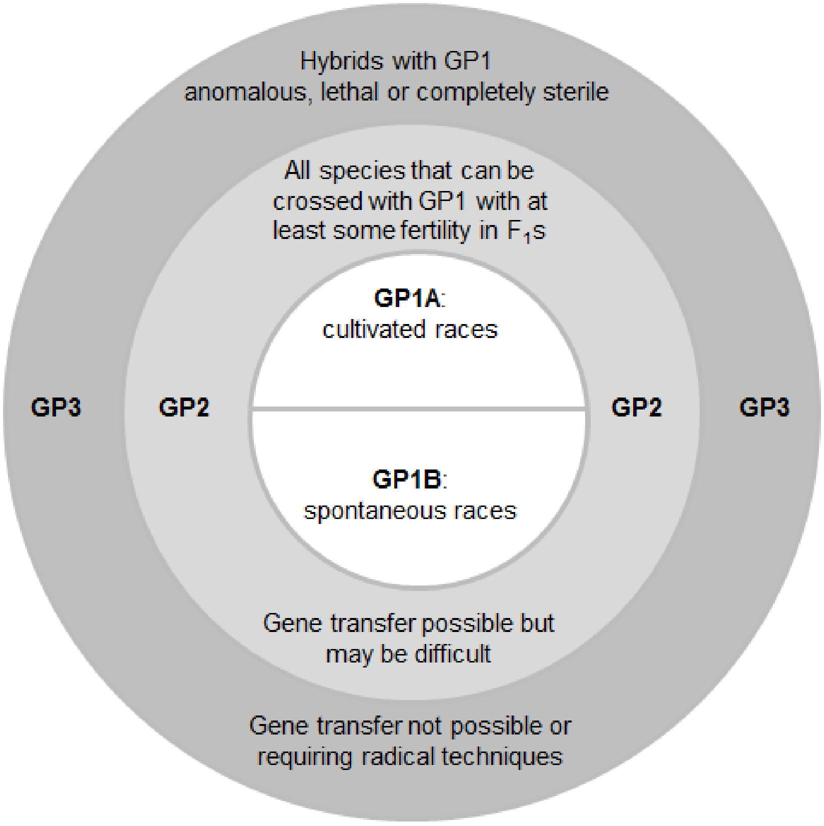

Figure 1.2 The gene pool concept (Adapted from: Harlan and de Wet (1971)).

Another useful approach for measuring crop and wild species relatedness is the taxon group (TG) concept devised by Maxted *et al.* (2006). This method is particularly beneficial when information on crossability between species is not available or these experiments have not yet taken place. The TG concept assumes that taxonomic distance is equivalent to genetic relatedness, although it is argued that this assumption does not always hold true, Maxted *et al.*, (2006) still reason that taxonomic distance can be a useful tool in determining CWR and crop relatedness.

Under the TG concept a taxon can be ranked as follows:

TG1A – crop

TG1B – same species as crop

TG2 – same series or section as crop

TG3 – same subgenus as crop

TG4 – same genus

TG5 – same tribe but different genus to crop

More recently, Wiersema *et al.* (2012) have developed a more modern approach to defining CWR, in keeping with the spirit of the GP concept defined by Harlan and de Wet (1971). Phylogenetic, taxonomic and crop science literature are widely consulted in order to assign closely related taxa into the following genetic-relative classes:

Primary – taxa that cross readily with the crop (or can be predicted to do so based on their taxonomic relationships), yielding (or being expected to yield) fertile hybrids with good chromosome pairing, making gene transfer through hybridisation simple.

Secondary – taxa that will successfully cross with the crop (or can be predicted to do so based on their taxonomic relationships), but yield (or would be expected to yield) partially or mostly sterile hybrids with poor chromosome pairing, making gene transfer through hybridisation difficult.

Tertiary – taxa that can be crossed with the crop (or can be predicted to do so based on their taxonomic relationships), but hybrids are (or are expected to be) lethal or completely sterile. Special breeding techniques, some yet to be developed, are required for gene transfer.

Graft stock – taxa used as rootstocks for grafting scions of a crop, or used as genetic resources in the breeding of such rootstocks.

1.3.2 Utilisation of CWR genetic resources

For over 60 years CWR have been used to improve crops with the rate of use increasing in recent years (Hajjar and Hodgkin, 2007; Maxted and Kell, 2009). Examples of beneficial traits CWR have provided crops with include: yield increases, salt tolerance, improved nutritional and health benefits, quality improvements such as taste, fertility restorers and cytoplasmic male sterility.

An example of CWR use in breeding for resistance to biotic factors is the breeding of *Aegilops tauschii* Coss. with a durum wheat cultivar, 'Langdon' with the resulting germplasm lines having Hessian fly resistance (Suszkiw, 2005). Another is the transference of a dominant gene for bacterial blight from *Oryza longistaminata* A. Chev. & Roehr. to cultivated rice (Brar and Khush, 1997).

CWR worth and contribution annually to improved food production and crop quality was first estimated by Pimental *et al.* (1997) at $115 billion globally - the equivalent of roughly $165 billion now (Tyack and Dempewolf, 2015) – however, NRC (2001) valued CWR contribution to crop productivity at only $1 billion annually. A more recent valuation was undertaken by PricewaterhouseCoopers for 32 priority crops vital for maintaining food security; they estimated that CWR contribution to improving these key crops was worth $68 billion per annum globally, with a potential to rise to $196 billion given predicted future crop production values. However, this recent estimate is only based upon a sample of four key crops and extrapolated out to other crops. This valuation can only rise, particularly as important economic crops such as coffee, whose CWR alone are estimated to be worth \$1.5 billion (Hein and Gatzweiler, 2006), are overlooked.

1.3.3 Threats to CWR

Like other wild plant species, CWR are increasingly threatened with extinction and genetic erosion in their natural habitats from the actions of humans. Kell *et al.* (2012) describe the main threats to CWR as: intensive livestock farming, tourism and recreation development and urbanisation. Ford-Lloyd *et al.* (2011) further add to these threats: land use change, climate change, alien invasive plants and over-harvesting in the wild. Jarvis *et al.* (2008) conducted a notable study on the effects of climate change on potato, peanut and cowpea CWR and found that distributions were likely to become highly fragmented and significantly reduced in the future, with wild peanuts being most affected with 24–31 taxa likely to go extinct and the remaining taxa losing over 85% of their current ranges. Climate change and human disturbance is thought to also bring along with it other perils, such as an increased prevalence of pest and pathogen outbreaks in both wild and cultivated plants (Anderson *et al.*, 2004; Fischer *et al.*, 2012). Changes in land use can cause species habitats to become fragmented and thus diminish the gene flow between populations, leaving CWR vulnerable to genetic erosion. CWR have four possible strategies for dealing with climate change: extinction, migration, phenotypic plasticity and environmental adaptation (Nicotra *et al.*, 2010).
Despite the known threats to CWR in their natural habitats very few have undergone IUCN Red List assessment; even CWR of major crops are absent, including wheat wild relatives - wild *Triticum* L. and *Aegilops* L. species. There are discrepancies at the global, regional and national level, with global assessments being particularly poor; however, CWR of Europe

have been assessed at the regional level (Bilz *et al.*, 2011). CWR such as *Mangifera rubropetala* (Kosterm.) are classed as extinct in the wild according to the IUCN Red List.

1.3.4 Policy covering CWR

The value of CWR as a provisioning ecosystem service has been recognised globally by several major bodies globally including the CBD, the Food and Agricultural Organisation (FAO) and the United Nations (UN) since the 1980s (Figure 1.3) Current global frameworks covering CWR conservation and sustainable use include:

- CBD Global Strategy for Plant Conservation 2011–2020, target 9 (CBD, 2011a): “70 per cent of the genetic diversity of crops including their wild relatives and other socio-economically valuable plant species conserved, while respecting, preserving and maintaining associated indigenous and local knowledge”.

- CBD Strategic Plan for Biodiversity 2011–2020, Aichi target 13 (CBD, 2011b): “By 2020, the genetic diversity of cultivated plants and farmed and domesticated animals and of wild relatives, including other socio-economically as well as culturally valuable species, is maintained, and strategies have been developed and implemented for minimising genetic erosion and safeguarding their genetic diversity”.

- UN Sustainable Development Goals, goal 2, target 2.5 (United Nations, 2016): “By 2020, maintain the genetic diversity of seeds, cultivated plants and farmed and domesticated animals and their related wild species, including through soundly managed and diversified seed and plant banks at the national, regional and international levels, and promote access to and fair and equitable sharing of benefits arising from the utilisation of genetic resources and associated traditional knowledge, as internationally agreed".

- FAO General Plan of Action (GPA) 2 for Plant Genetic Resources for Food and Agriculture, priority activity 4 (FAO, 2011a): "Promoting *in situ* conservation and management of crop wild relatives and wild food plants".

- FAO International Treaty on Plant Genetic Resource for Food and Agriculture (ITPGRFA), article 5 (FAO, 2001): "Each Contracting Party shall… survey and inventory plant genetic resources for food and agriculture..., promote the collection of plant genetic resources for food and agriculture…, promote *in situ* conservation of wild crop relatives…, cooperate to promote the development of an efficient and sustainable system of *ex situ* conservation…and monitor the maintenance of the viability, degree of variation, and the genetic integrity of collections of plant genetic resources for food and agriculture".

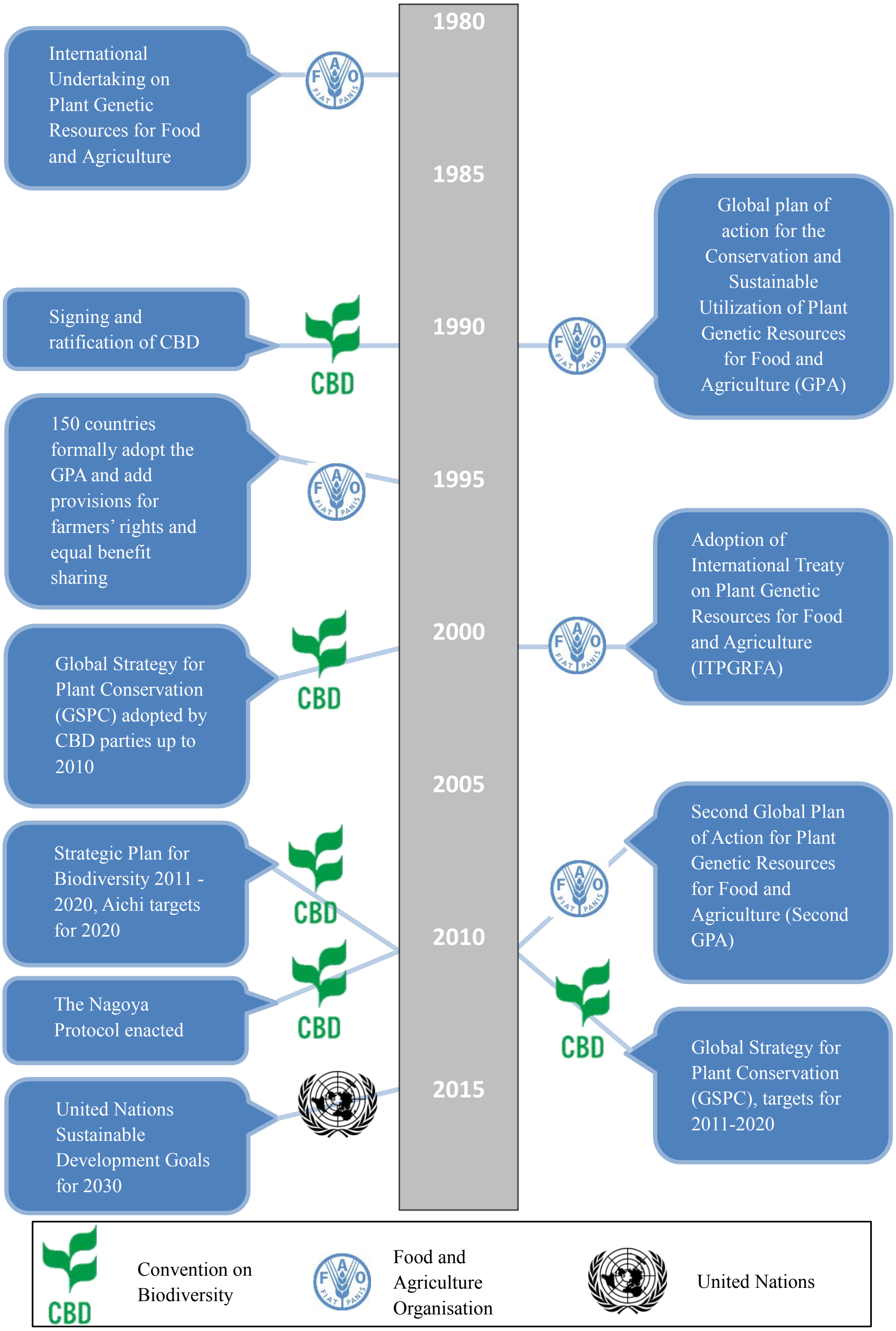

Figure 1.3 Timeline of key global policies regarding CWR conservation and utilisation

1.3.5 Systematic conservation of CWR

CWR conservation to date has been opportunistic and driven by singular interests rather than following a systematic process. Figure 1.4 outlines the process of systematic CWR conservation and how it can be achieved.

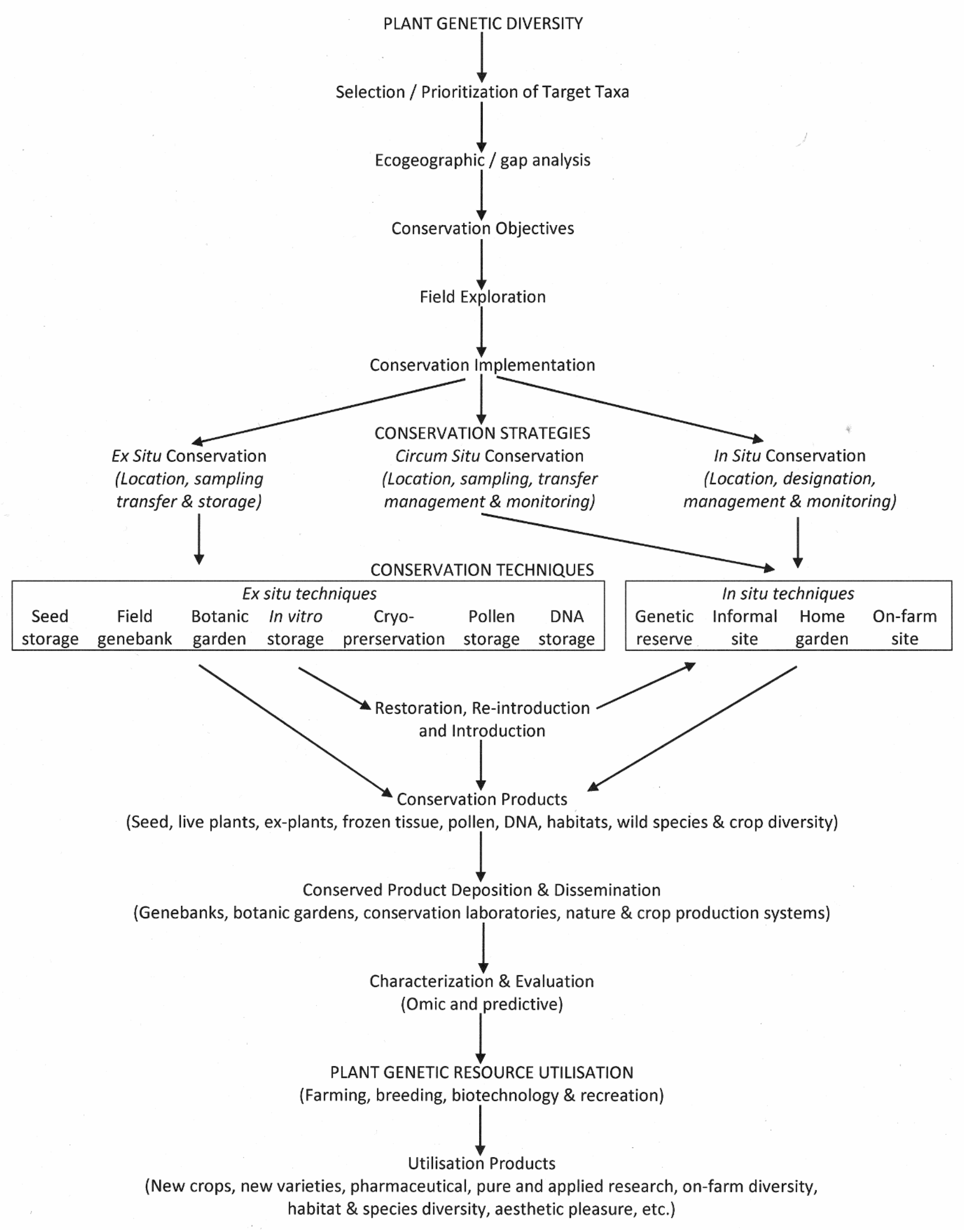

Figure 1.4 Methodology for systematic PGR conservation (Extracted from Maxted *et al.*, 2016)

1.3.6 CWR gap analysis

Gap analysis involves analysing the sufficiency of existing conservation methods for target taxa and identifying where taxa are under-represented to improve conservation actions. Maxted *et al.* (2008a) developed a gap analysis methodology to measure CWR conservation effectiveness involving four steps:

1. Circumscription of target taxa
2. Natural diversity assessment (assessments can include taxonomy, ecogeographic/environmental, threat and genetic diversity)
3. Assessment of current *in situ* and *ex situ* conservation strategies
4. Identifying gaps in current conservation strategies and re-formulation to incorporate gaps into strategies

Selection of target taxa depends on several factors such as stakeholder interests, adoption of a floristic or monographic approach, economic value of taxa, cultural value and geographic study area. A recent rise in the number of national checklists and inventories has enabled a number of national and regional gap analyses, and development of CWR conservation strategies (Idohou *et al.*, 2012; Rubio Teso *et al.*, 2013; Phillips *et al.*, 2014; Fielder *et al.*, 2015). Kell *et al.* (2015) suggest that the closeness of genetic relationship between CWR and crop, threat level of CWR and socio-economic utilisation of CWR are the most important criteria to consider in selecting target taxa for conservation planning, mainly due to their importance in crop breeding. In the past decade examples of gap analysis studies based upon CWR taxa have increased greatly (Ramírez-Villegas *et al.*, 2010; Para-Quijano *et al.*, 2007; Vincent *et al.*, 2012; Moray *et al.*,2014; Kantar *et al.*, 2015; Castañeda-Álvarez *et al.*, 2016a).

Species distribution models (SDMs) have been increasingly used in gap analysis studies, particularly since the creation of the MaxEnt software (Phillips *et al.*, 2006) which produces high quality predictive models based upon presence only data and a set of environmental predictors. SDMs have proven successful at predicting novel areas for *ex situ* sampling, with examples for *Capsicum flexuosum* Sendtn (Jarvis *et al.*, 2005) and *Lactuca* L. species (Cobben *et al.*, 2014). To assess the effectiveness of current conservation strategies, the results from SDMs are compared to the numbers and locations of germplasm accessions conserved *ex situ* to assess representativeness across the CWR range, whilst for *in situ* gap analysis SDMs or occurrence points are compared to protected areas to assess coverage within the study area. The majority of gap analyses employing SDMs are studying *ex situ* conservation; however, there is a growing trend of incorporating SDMs into *in situ* gap analysis too, particularly to quantify the effects of climate change on taxon distribution (Allnutt *et al.*, 2012; Lessmann *et al.*, 2014). The final phase in CWR gap analysis is to reformulate conservation strategies to fill the gaps identified in step 3 (Maxted *et al.*, 2008b). For *ex situ* gap analysis this involves identifying priority areas for further *ex situ* collecting and for *in situ* gap analysis, reserve planning algorithms can be used to find potential areas to establish new genetic reserves, within and outside of the existing protected area network. Conservation planning and gap analysis are benefiting from the steadily growing amount of easily accessible and freely available information related to plant conservation, such as occurrence record repositories like GBIF; environmental modelling layers such as those available from the Worldclim repository and the ISRIC-World Soil Information database; environmental modelling software such as MaxEnt and the BIOMOD package in R; GIS modelling software like QGIS; and, reserve planning software such as Marxan and Zonation. As society becomes ever more digitised, no doubt greater resources for conservation planning will become available online for researchers, particularly in the field of genetics where the reduction in costs of genomics will yield more data on genetic diversity of CWR individuals and populations.

1.3.7 Conservation techniques

Ex situ conservation involves the protection and maintenance of biodiversity elements outside of their natural environment (CBD, 1992). *Ex situ* CWR conservation is the systematic sampling and collecting of wild germplasm from natural habitats and removal and safe storage of collected material. There are several types of storage methods available for collected germplasm *ex situ*. For example seeds can be stored as active accessions, which imply short term conservation, by storage of seeds for regeneration, study and breeding, in the case of orthodox seeds, or for recalcitrant seeds, seeds can be stored short term in vitro. For long term or inactive storage, orthodox seeds can be stored at sub-zero temperatures in genebanks such as the Svalbard Global Seed Vault, and recalcitrant seeds can be cryo-preserved for long term storage. CWR can also be conserved *ex situ* in botanical gardens or field genebanks where they can be further studied and protected from extinction; this method is particularly useful for species that are difficult to store in conventional seed genebanks, such as *Coffea* L. species.

According to the FAO, only 25–30% of all plant accessions held in genebanks are unique whilst the remaining accessions are duplicated material from regeneration and distribution of germplasm between genebanks (FAO, 2010). Furthermore, the FAO (2010) report that only 10% of all accessions held in genebanks worldwide are CWR taxa, similarly in a study of EURISCO germplasm accessions, Dias *et al.* (2012) reported that only 9% of the material stored was from wild species with the rest being of cultivated origin. This vast inequality in *ex situ* conservation between cultivated and wild species may seem counterintuitive, however, in the past breeders have preferred to use cultivated material in order to improve crops, due to fewer crossing barriers and reduced chance of linkage drag. More recently plant breeders have called for access to greater genetic diversity (Tanksley and McCouch, 1997; McCouch *et al.*, 2013) thus highlighting the need for greater conservation and access to novel CWR germplasm.

One major benefit of *ex situ* conservation is the safeguarding of genetic material that could easily become threatened or extinct in the wild, thus acting as a safety net for CWR loss and a potential source of material for re-introduction to habitats where the species may once have existed (Maxted *et al.*, 1997c). Another key benefit of *ex situ* conservation in the case of germplasm genebanks is the ease of access and availability of CWR material for plant breeders, compared to the narrow window of opportunity to collect plant germplasm in the wild. The relatively low cost, in comparison to *in situ* conservation, of conserving species *ex situ* is also widely agreed to be the simplest, most cost-effective method of securing CWR. The disadvantages to solely relying on *ex situ* conservation are that genetic diversity can be lost over time through regeneration of *ex situ* material and that *ex situ* conservation halts the evolutionary process of CWR, thus only providing a snap shot of genetic diversity in time (Maxted *et al.*, 1997c).

The CBD (1992) defines *in situ* conservation as: “the conservation of ecosystems and natural habitats and the maintenance and recovery of viable populations of species in their natural surroundings and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties”. Approaches for *in situ* conservation of CWR usually involve genetic reserves, on farm monitoring or home garden management. These approaches require substantial stakeholder involvement to set up, maintain and monitor for long term protection. In the past *in situ* conservation has mainly been focussed on rare or threatened or charismatic wild species (Heywood and Dulloo, 2005), with species of great utility like CWR being undervalued. In the PGR community, *ex situ* conservation has been the preferred method of conserving CWR (Maxted, 2015), no doubt due to the relative ease of collecting and storing high volumes germplasm off site, however, the attention is now slowly switching to *in situ* conservation to address this imbalance and ensure long term CWR access and protection (FAO, 2011a, 2013, 2014).

Although more costly to maintain and establish, *in situ* conservation does have several key benefits that *ex situ* conservation does not provide. *In situ* actions allow for the continual development and adaptation of CWR to changing environments leading to new traits which can be utilised via plant breeding. Conserving *in situ* also allows CWR to maintain relationships with pollinators and fellow niche members, preserve CWR habitat and conserve multiple species in one area. Furthermore, for some taxa, in particular recalcitrant germplasm, it is difficult to store and save regenerative material *ex situ*, therefore *in situ* actions are preferred (Maxted *et al.*, 1997c). However, situations like the ongoing civil war in Syria can jeopardise *in situ* conservation actions and protected areas, highlighting the need for *ex situ* backup collections.

Ford-Lloyd and Maxted (1993) state that a truly robust conservation strategy needs to employ complementary conservation; that is a mixture of *in situ* actions backed up by *ex situ* collections of regenerative material. This is to ensure habitat preservation, maintain evolutionary adaptation of taxa and provide a safety net of germplasm stored off site for potential re-introduction to the wild if necessary and study and use by plant scientists and breeders.

1.3.8 Focus on *in situ* conservation of CWR and protected areas

Due to the preference of the CWR community for *ex situ* conservation because of its relative ease, and the multiple barriers to *in situ* conservation (e.g. political and administrative issues, stakeholder participation, funds for establishing and maintaining, acquisition of land for new reserves), few areas globally have been designated as reserves for the conservation of CWR. Table 1.1 highlights examples of CWR protection *in situ*, including the site location and taxa conserved. One such example is the Erebuni State Natural Reserve near Yerevan, Armenia established in 1981 which is known for its richness of wild relatives of cereals such as *Hordeum bulbosum* L., *Secale vavilovii* Grossh., *Triticum urartu* Tumanian ex Gandilyan and several *Aegilops* taxa *(*Avagyan, 2007).

Table 1.1 Examples of CWR *in situ* conservation and reserves throughout the world

CWR Species	**Reserve**	**Region**	**Country**	**Source**
Potato CWR	Villavicencio Natural Reserve	Mendoza	Argentina	Marfil *et al.* (2015)
Triticum boeoticum Boiss., *T. urartu* Tumanian ex Gandilyan, *T. araraticum* Jakubz.	Erebuni Reserve	Yerevan	Armenia	Avagyan (2007)
Phaseolus L.	Central valley		Costa Rica	Baudoin *et al.*

				(2008)
Coffea L.	Numerous reserves		Ethiopia	Hoyt (1998)
Wheat and fruit tree CWR	Unknown	Caucasus	Former Soviet Union	Hoyt (1998)
Apple, peach, and pistachio CWR	Unknown	Caucasus	Former Soviet Union	Tuxill and Nabhan (1998)
Teosinte CWR	Unknown		Guatemala	Wilkes (1993)
Citrus indica Tanaka	Garo Hills Biosphere Reserve		India	Hodgkin and Arora (1999)
Triticum turgidum L. subsp. *dicoccoides* (Korn. ex Asch. & Graebn.) Thell.	Ammiad reserve	Eastern Galilee	Israel	Anikster *et al.* (1997)
Walnut, apple, pear and *Prunus* L. CWR	Sary-Chelek		Kyrgyzstan	Hoyt (1998)
Medicago L.; *Vicia* L.; *Trifolium* L.; *Lathyrus* L.; *Lens* Mill.; *Triticum* L.; *Avena* L.; *Hordeum* L.; *Aegilops* L.; *Allium* L.; *Prunus* L.; *Pyrus* L.; *Pistacia* L.; *Olea* L.	Abu Taha, Sale-Rsheida, Ajloun, Wadi Sair		Lebanon, Syria, Jordan, Palestinian Territories	Al-Atawneh *et al.* (2008)
Coffea mauritiana Lam., *C. macrocarpa* A. Rich., *C. myrtifolia* (A. Rich. ex DC.) J.-F. Leroy	Black River Gorges National Park		Mauritius	Dulloo *et al.* (1999)
Zea diploperennis H. H. Iltis *et al.*, *Phaseolus vulgaris* L., *Phaseolus coccineus* L.	MAB Sierra de Manantlán Biosphere Reserve		Mexico	UNESCO (2007)

Zea nicaraguensis H. H. Iltis & B. F. Benz	Deltas del Estero Real y Llanos de Apacunca.		Nicaragua	Ramsar (2016)
Potato CWR	Parque de la Papa	Cuzco	Peru	Argumedo and Stenner (2008)
Wild beet (*Beta patula* Aiton)	Desertas Is.		Portugal	Pinheiro de Carvalho *et al*. (2012)
Triticum turgidum subsp. *dicoccoides*, *T. monococcum* L., *Ae. tauschii* Coss., *Ae. speltoides* Tausch	Ceylanpinar		Turkey	Karagöz (1998)
Castanea sativa Mill., *Prunus cerasifera* var. *divaricata* (Ledeb.) L. H. Bailey	Kazdağ		Turkey	Kűçűk *et al.* (1998)
Pistachio, apricot, almond and fodder grass CWR	Kopet Mts.		Turkmenistan	Hoyt (1998)
Allium geyeri S. Watson and *A. fibrillum* M. E. Jones	Great Basin, Washington State		USA	Hannan and Hellier (1999); Hellier (2000)
Vitis rupestris Scheele, *V. shuttleworthii* House, *V. monticola* Buckley	Witchita Mountains and Ouachita National Forest, Oklahoma, Clifty Creek, Missouri		USA	Pavek *et al*. (2003)
Capsicum L.	Coronado National Forest		USA	Tuxill and Nabhan

(1998)

The IUCN defines a protected area as “A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Dudley, 2008). Maxted *et al.*, (2008), suggest that a more productive method of establishing sites for CWR conservation is to site them in existing protected areas and update management plans accordingly to include CWR protection and monitoring. This removes the need to acquire new land for reserves, management and legal protection (if any) is already in place and a long term conservation ethos is present, significantly lowering the barriers to successful *in situ* conservation (Maxted *et al.*, 2008a). Examples of where this approach has been taken include an Argentinian protected area — Villavicencio Natural Reserve — in the Mendoza province that was identified as a priority area for South American potato CWR. Population monitoring of wild potatoes in this reserve has been introduced, along with education about PGR and CWR inclusion in protected area management plans (Marfil *et al.*, 2015). Another example of CWR genetic reserves established within existing protected areas is the Deltas del Estero Real y Llanos de Apacunca Ramsar protected area which in 1996 established a CWR reserve to protect and manage populations of the endemic wild teosinte species *Zea nicaraguensis* Iltis & Benz (Ramsar, 2016). The majority of the sites listed in Table 1.1, however, do not meet the standards for genetic conservation reserves-systematic CWR prioritisation, demographic surveying and genetic diversity analysis- (Iriondo *et al.*, 2012), calling into question their effectiveness at conserving genetic diversity of CWR. A global network of CWR genetic reserves (incorporating existing sites), following the standards of Iriondo *et al.* (2012) would greatly increase the representativeness of CWR in reserves worldwide and maximise genetic diversity covered, thus improving CWR *in situ* conservation status dramatically.

The current global protected area network covers 15.4% of the terrestrial world (Juffe-Bignoli *et al.*, 2014) and has the potential to protect species populations and preserve eco-systems when adequate monitoring and management is in place (Butchart *et al.*, 2010; Geldmann *et al.*, 2013). However, several studies have shown that the current protected area network poorly represents the breadth of biodiversity in the world; with 29% of all terrestrial ecoregions having less than 5% of their range covered by protected areas and 85% of all threatened birds, mammals and amphibians having insufficient populations in protected areas to enable long term survival (Venter *et al.*, 2014, Watson *et al.*, 2014). The unsuitability of the protected area network for biodiversity conservation is further compounded in that additional sites added in the last 20 years have been predominantly land with low economic value, low human density; poorly targeting areas with exceptionally high levels of biodiversity (Joppa and Pfaff, 2009). Additionally, Leverington *et al.* (2010) state that 60% of protected areas are underfunded and only 20–50% are effectively managed (Laurance *et al.*, 2012). Existing protected areas are also increasingly under pressure from outside influences such as harmful industrial activities like mining and agribusiness (DeFries *et al.*, 2005; Duran *et al.*, 2013; WWF, 2016) and protected area downgrading, downsizing and degazettement (PADDD) (Mascia *et al.*, 2011). With protected areas being described as increasingly isolated islands of biodiversity (MacKinnon, 2016) there is an increasing need to conserve outside of formalised protected areas, to create corridors of biodiversity between protected areas to maintain gene flow between populations (Naughton-Treves *et al.*, 2005; Maxted and Kell, 2009). One such underutilised approach is the Community Conservation Area (CCA) method, in which local or indigenous people help to sustainably manage resident biodiversity – this has been implemented for potato CWR and landraces in the Parque de la Papa in Peru, where the indigenous Quechua people maintain traditional farming practices, traditions and culture whilst conserving and utilising landraces and CWR. Another approach that has been proposed is the conservation of disturbed habitats, such as roadside verges, where many ruderal CWR species are known to exist, however little practical headway has been made with how this could be successfully implemented (Maxted and Kell, 2009; Maxted *et al.*, 2016).

1.4 Research objectives

The untapped potential and importance of CWR for breeding more resilient, high yielding, nutritious and overall genetically diverse crops is undeniable. However, it is also clear that *in situ* conservation of these species has been fragmentary and lacked a clear methodical approach. The need for systematic *in situ* CWR conservation is now paramount in order to increase the availability of a rich range of plant genetic diversity long term for crop improvement programmes; prevent the loss of vulnerable CWR species and their habitats; reduce the loss of genetic diversity within CWR species and achieve global CWR protection and utilisation targets (Maxted *et al.*, 2012; Dempewolf *et al.*, 2014). This is particularly urgent due to the pressures of climate change, the need to sustainably and efficiently adapt our agricultural systems to feed a growing human population and the time it takes to develop new crop varieties for use by farmers- sometimes up to 30 years (Jones *et al.*, 2014).

This thesis aims to provide a basis for improved food security, whilst mitigating climate change and biodiversity loss, by systematically identifying and prioritising CWR of global importance for crop breeding and advancing knowledge on priority geographical areas for *in* *situ* CWR conservation globally. The major questions which will be addressed in the thesis are as follows:

1. Which CWR species are most important for maintaining and improving food security?
2. Where are the best sites globally for conserving priority CWR species long term and their breadth of genetic diversity?
3. Where are there ongoing *in situ* conservation activities globally into which CWR conservation could be introduced?
4. Are CWR rich areas coincident with other geographical areas of high biodiversity?
5. Do CWR rich areas have a similar geographical distribution to centres of crop domestication/diversity?

1.5 Thesis outline

To address each of the preceding aims the thesis is divided into the following research chapters:

1. A prioritised crop wild relative inventory to help underpin global food security (Chapter 2)

   Whilst there have been many papers and projects addressing CWR conservation using a floristic approach on the national (Berlingeri and Crespo, 2012; Idohou *et al.*, 2012; Rubio Teso, *et al.*, 2013; Phillips *et al.*, 2014; Fielder *et al.*, 2015) or regional scale (Kell *et al.*, 2008); or using a monographic approach for individual species (Davies *et al.*, 2012) or CWR from singular/small groups of crop gene pools (Kantar *et al.*, 2015;

Maxted and Kell, 2009; Vincent *et al*., 2012), there is still a need for a global analysis of all CWR related to our most important crops (Maxted *et al*., 2012; Dempewolf *et al*., 2014). However, for many crops, the closest CWR have yet to be determined. The research presented in Chapter 2 fills this knowledge gap as a first step towards the global systematic conservation of CWR, by documenting for the first time, the priority CWR of all major crops important for global food security. The research questions considered in this chapter include: what are the World's most important crops?; what constitutes a priority CWR?; what is the best method for dealing with crops which lack both hybridisation data and prioritisation concepts?; what are the priority CWR for the World's most important crops and where are they found?

2. Global priorities for *in situ* conservation of wild plant genetic resources: towards the establishment of a global network of crop wild relative reserves (Chapter 3 and Appendix 1)

   A lack of knowledge about the geographical distribution, genetic diversity and relation to crops of globally important CWR has previously prevented any attempts at large scale *in situ* conservation planning. As such, the few sites that have been developed for CWR conservation have usually been selected via national analysis, by analysing a small number of key crop gene pools or not based on any systematic analysis at all. Additionally, very few of these existing sites are thought to meet the minimum requirements for a CWR genetic reserve set out by Iriondo *et al.* (2012), thus bringing into question their long term effectiveness. Chapter 3 investigates the possibilities of a global network of *in situ* genetic reserves which conserve the priority CWR of globally important crops identified in Chapter 2. The complexity and realism of the reserve planning problem is increased by modelling the effects of climate change on individual species potential distributions and by maximising the use of the existing global PA network. The research questions considered in this chapter include: where are the richest geographical areas for CWR?; which eco-geographical niches do these CWR inhabit?; which existing protected areas contain priority CWR?; and which is the most effective network of sites globally that conserve maximal CWR genetic diversity?

3. A comparison of crop wild relative hotspots with biologically and ecologically important geographical regions; a case study with Myers' biodiversity hotspots (Chapter 4)
   Economic resources for conservation are often short term and limited, therefore conservation actions should be focussed in areas that hold the most biodiversity and can maximise conservation returns. Chapter 4 first defines then examines the geographical differences between CWR hotspots and a well-established concept on biologically important areas. Possibilities for *in situ* CWR conservation within ongoing conservation efforts in Myers' Biodiversity Hotspots are studied as an optional route in to which we can further complementary conservation, by the promotion of CWR *in situ* protection, alongside ongoing conservation activities. The research questions considered in this chapter include: where are the CWR rich global hotspots geographically?; how many priority CWR exist in Myers' biodiversity hotspots?; how many priority sites for *in situ* conservation (identified in Chapter 3) exist in Myers' biodiversity hotspots?; and, which areas of Myers' biodiversity hotspots can be targeted for CWR *in situ* conservation?

4. A comparison of global crop wild relative hotspots with theories on centres of plant domestication and diversity (Chapter 5)

   Throughout CWR conservation planning literature and strategy recommendations, Vavilov centres of diversity are quoted as being key geographical areas in which to concentrate conservation efforts (Rubenstein *et al.*, 2005; Maxted and Kell, 2009; Stolten *et al.*, 2010; Ford-Lloyd *et al.*, 2011; Kell *et al.*, 2015). Chapter 5 examines whether Vavilov centres of diversity are analogous to areas of CWR diversity and whether conservation in Vavilov centres would fully represent the wealth of CWR worldwide. Furthermore, we examine areas which may not be covered by well-known concepts on centres of crop domestication and diversity but contain significant CWR richness. The research questions considered in this chapter include: do CWR hotspots align with Vavilov centres of diversity?; to what extent do CWR hotspots overlap other key concepts on centres of plant domestication and diversity?; are there any areas rich in CWR diversity where there are no centres of crop diversity? and, which concept on centres of crop domestication and diversity, if any, is most similar to CWR hotspots and areas of high species richness?

CHAPTER 2

A prioritised crop wild relative inventory to help underpin global food security

The work presented in this chapter has been published in the journal Biological Conservation:

Vincent, H., Wiersema, J., Kell, S., Fielder, H., Dobbie, S., Castañeda-Álvarez, N.P., Guarino, L., Eastwood, R., León, B. and Maxted, N. (2013) A prioritised crop wild relative inventory to help underpin global food security. Biological Conservation 167, 265─275.

Author contributions:

Conceived and designed the study: **HV**, NM

Data collection and preparation: **HV**, JW, HF, SD, BL

Creation of database: **HV**

Performed analysis: **HV**

Analysed results: **HV**

Wrote the paper: **HV**

Critically reviewed the paper: **HV**, NM, JW, SK, HF

2.1 Abstract

The potentially devastating impacts of climate change on biodiversity and food security, together with the growing world population, means taking action to conserve CWR diversity is no longer an option – it is an urgent priority. CWR are species closely related to crops, including their progenitors, which have potential to contribute traits for crop improvement. However, their utilisation is hampered by a lack of systematic conservation which in turn is due to a lack of clarity over their identity. We used gene pool and taxon group concepts to estimate CWR relatedness for 173 priority crops to create the Harlan and de Wet inventory of globally important CWR taxa. Further taxa more remotely related to crops were added if they have historically been found to have useful traits for crop improvement. The inventory contains 1667 taxa, divided between 37 families, 108 genera, 1392 species and 299 sub-specific taxa. The region with the highest number of priority CWR is western Asia with 262 taxa, followed by China with 222 and south eastern Europe with 181. Within the primary gene pool, 242 taxa were found to be under-represented in *ex situ* collections and the countries identified as the highest priority for further germplasm collection are China, Mexico and Brazil. The inventory database is web-enabled (http://www.cwrdiversity.org/checklist/) and can be used to facilitate *in situ* and *ex situ* conservation planning at global, regional and national levels.

2.2 Introduction

The human population is expected to reach 9.6 billion by 2050 (UN, 2014), with the largest increases in Africa and Asia where there is also the greatest undernourishment globally (FAO, IFAD and WFP, 2015). Food security worldwide is further jeopardised by the potentially disruptive and detrimental effects of climate change on crop production (Schmidhuber and Tubiello, 2007; Lobell *et al*., 2008; Palm *et al*., 2010). One under-developed strategy for improving global food security for the present and future is the systematic targeting and use of crop wild relatives (CWR) in breeding new climate resilient and higher yielding crop varieties (FAO, 2012). Maxted *et al*. (2006) define a CWR as: ‘‘a wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop’’. CWR contain a great breadth of genetic diversity having not passed through the genetic bottlenecks of domestication (Vollbrecht and Sigmon, 2005; van de Wouw *et al*., 2009) and adapting to a wide range of habitats, including those considered marginal and inhospitable (Ford-Lloyd *et al*., 2011). For over six decades plant breeders have utilised beneficial traits from CWR in breeding new resistant crop varieties, including resistance to abiotic and biotic stresses, improved yield and enhanced quality (Haijar and Hodgkin, 2007); however, CWR use has not been systematic and only implemented for a small number of crops (Maxted *et al*., 2012). Climate change-induced environmental changes are undoubtedly impacting the conditions under which our crops grow. Already, many crop varieties are being replaced with stress tolerant varieties to ensure the agricultural viability of the crop in the same locations (Jones *et al*., 2003; Duveiller *et al.*, 2007; Deryng *et al.*, 2011; Li *et al.*, 2011; Luck *et al.*, 2011; Yadav *et al.*, 2011). The ability of breeders to increase or even sustain crop yield and quality in the face of dynamic biotic and abiotic threats without greater use of exotic germplasm has been questioned (Feuillet *et al.*, 2008); therefore, CWR are an obvious target to aid crop improvement and food security. CWR, like other wild plant species, are experiencing widespread genetic erosion and even extinction as a result of direct or indirect human-mediated environmental changes (Jarvis *et al.*, 2008; Bilz *et al.*, 2011).

A recent study to undertake IUCN Red List assessments of 572 European CWR species in 25 crop gene pools/groups (Bilz *et al.*, 2011; Kell *et al.*, 2012) found that at least 11.5% of the species are threatened — 3.3% of them being Critically Endangered, 4.4% Endangered and 3.8% Vulnerable — and that a further 4.5% of the species are classified as Near Threatened. These percentages are likely to increase further following reassessment of the species that are currently classified as Data Deficient (Kell *et al.*, 2012). With a global estimated value of $115 billion annually for the introduction of new genes from CWR to crops (Pimentel *et al.*, 1997), it might be expected that CWR would already be effectively conserved and readily available for use by breeders. However, conservation of CWR diversity has yet to be addressed systematically. Despite knowledge on the broad range of genetic diversity within CWR and their value for crop improvement, only 2–10% of global *ex situ* gene bank accessions are CWR taxa; furthermore, these collections represent only a small fraction of all global CWR taxa (Maxted and Kell, 2009).

In situ CWR conservation has also been neglected. The majority of global protected areas were originally established to conserve threatened, rare or charismatic wildlife or iconic landscapes (Maxted, 2003; Heywood and Dulloo, 2005; Watson *et al.*, 2014); sites targeted at CWR conservation are rare. Although CWR populations are conserved *in situ* where their inclusion is coincident with other protected area priorities, such as when they are recognised as a nationally rare or threatened species, their conservation per se and specifically the conservation of their genetic diversity is currently not deemed a priority within the protected area community (Maxted, 2003; Vincent *et al.*, 2012). The requirement for systematic CWR conservation has been recognised by major bodies such as the Food and Agriculture Organisation of the United Nations in the International Treaty on Plant Genetic Resources for

Food and Agriculture (FAO, 2001) and in a number of other international treaties and policy documents. The Convention on Biological Diversity recognises CWR conservation as a global priority (FAO, 2001, 2011a; CBD, 2010a, 2010b). The Global Strategy for Plant Conservation 2011–2020 (CBD, 2010a) states in Target 9 that ‘’70 per cent of the genetic diversity of crops including their wild relatives and other socio-economically valuable plant species [should be] conserved’’, while the CBD Strategic Plan (CBD, 2010b) Target 13 called for ‘‘By 2020, the status of crop and livestock genetic diversity in agricultural ecosystems and of wild relatives [will have] been improved’’. To address the requirement for systematic CWR conservation, the Global Crop Diversity Trust (GCDT) launched the ‘‘Adapting agriculture to climate change: collecting, protecting and preparing crop wild relatives’’ project (GCDT, 2013) with the objectives of identifying global priority CWR, developing and implementing an *ex situ* conservation action plan for priority species, and promoting the use of the conserved diversity in crop improvement programmes.

This paper describes the creation of a global priority CWR inventory, including key ancillary data. It also reports on the taxonomic content of the inventory, the geographical distribution of the taxa with particular reference to the Vavilov centres of crop diversity (Vavilov, 1935), their potential use in plant breeding for crop improvement, their current *ex situ* conservation status, and their seed storage behaviour.

2.3 Materials and Methods

2.3.1 Creation of the priority CWR inventory

To create the inventory, first it was necessary to produce a list of genera containing the most socio-economically important global food crops. Two sources of the most important food crops are the International Treaty on Plant Genetic Resources for Food and Agriculture Supplementary Annex 1 (FAO, 2001) and the major and minor food crops of the world listed by Groombridge and Jenkins (2002); these were combined to generate a list of genera containing the world's most important crop species. Table 2.1 lists the 92 genera containing crops which were used to create the initial version of the global priority CWR inventory. Many of the target genera contain multiple crops; for example the genus *Phaseolus* contains lima bean, tepary bean and common bean. Therefore, it was also necessary to compile a list of all crops included within the target genera; this list was compiled using the list of major and minor food crops (Groombridge and Jenkins, 2002) and Mansfeld's encyclopedia of agricultural and horticultural crops (Hanelt and Institute of Plant Genetics and Crop Plant Research, 2001). A practical decision was made to exclude minor crops with a restricted cultivation range at this stage, but these may be included in future iterations of the CWR inventory.

Table 2.1 Global priority list of 92 CWR genera. * = Genera included International Treaty on Plant Genetic Resources for Food and Agriculture (25).

Agropyron Gaertn. *	*Dioscorea* L.	*Panicum* L.
Allium L.	*Diplotaxis* DC. *	*Pennisetum* Rich.
Ananas Mill.	*Echinochloa* P.Beauv.	*Persea* Mill.
Armoracia G.Gaertn., B.Mey & Scherb.	*Elaeis* Jacq.	*Phaseolus* L.

*		
Arachis L.	*Elettaria* Maton	*Phoenix* L.
Artocarpus J.R.Forst. & G.Forst. *	*Eleusine* Gaertn.	*Pimenta* Lindl.
Asparagus L. *	*Elymus* L. *	*Piper* L.
Avena L.	*Eruca* Mill. *	*Pistacia* L.
Barbarea W.T.Aiton *	*Ficus* L.	*Pisum* L.
Bertholletia Bonpl.	*Fragaria* L.	*Prunus* L.
Beta L.	*Glycine* Willd.	*Pyrus* L.
Brassica L.	*Gossypium* L.	*Raphanus* L. *
Cajanus Adans.	*Helianthus* L.	*Ribes* L.
Camellia L.	*Hordeum* L.	*Rorippa* Scop. *
Capsicum L.	*Ilex* L.	*Saccharum* L.
Carica L.	*Ipomoea* L.	*Secale* L.
Carthamus L.	*Isatis* L. *	*Sesamum* L.
Chenopodium L.	*Juglans* L.	*Setaria* P.Beauv.
Cicer L.	*Lablab* Adans.	*Sinapis* L. *
Citrullus Schrad.	*Lactuca* L.	*Solanum* L.
Citrus L.	*Lathyrus* L. *	*Sorghum* Moench
Cocos L.	*Lens* Mill.	*Spinacia* L.
Coffea L.	*Lepidium* L. *	*Theobroma* L.
Colocasia Schott	*Lupinus* L.	*Triticum* L.
Corylus L.	*Malus* Mill.	*Vicia* L.
Crambe L. *	*Mangifera* L.	*Vigna* Savi
Cucumis L.	*Manihot* Mill.	*Vitellaria* C.F.Gaertn.
Cucurbita L.	*Medicago* L.	*Vitis* L.
Cynara L.	*Musa* L.	*Xanthosoma* Schott
Daucus L.	*Olea* L.	*Zea* L.
Digitaria Haller	*Oryza* L.	

The next step was to identify the priority CWR within each crop genus. There has been considerable debate over which criteria should be considered when prioritising species for conservation (Fitter and Fitter, 1987) and specifically for prioritising CWR species (Heywood and Dulloo, 2005; Ford-Lloyd *et al.*, 2008; Villard and Jonsson, 2009; Magos Brehm *et al.*, 2010; Hunter and Heywood, 2011). However, most commonly, CWR prioritisation is based on three main criteria: (a) relative socio-economic importance of the related crop, (b) potential use for crop improvement (i.e., ease of crossability with the related crop or previously reported known use or potential use in crop improvement programmes), and (c) threatened status. Some or all of these criteria may be used in a variety of combinations, either independently or sequentially (Maxted and Kell, 2009; Magos Brehm *et al.*, 2010; Kell *et al.*, 2012). In developing the global priority CWR inventory, criteria (a) and (b) were deemed most important as they are directly related to the raison d'etre for defining CWR (i.e., their use for crop improvement). CWR taxa may be scored for these prioritisation criteria by collating information from published crop and CWR crossing experiments and by published concepts of the ease of crossability between a crop and CWR (Maxted *et al.*, 2006). The most commonly used prioritisation concept, the gene pool (GP) concept (Harlan and de Wet, 1971), is relatively objective and widely accepted. However, knowledge of whether each CWR is able to cross with its related crop is lacking for many crop complexes and in these cases the taxon group (TG) concept (Maxted *et al.*, 2006) can be used as a proxy. This concept is based on the assumption that the taxonomic classification (including both traditional and phylogenetic methods) is strongly linked to genetic relatedness, and when gene pool and taxon group concepts are compared for known crop complexes, this assumption seems well founded (Maxted *et al.*, 2006). In addition, a third concept was applied in this study: the 'provisional gene pool concept' (PGP). This was used when there was no formally published gene pool concept and when taxonomic treatments lacked subgeneric information, but there was published crossability evidence between the crop and related taxa. Table 2.2 details the three concepts of potential crossability between the CWR and target crop within a given crop complex. One of the three prioritisation concepts was applied to each crop complex and the priority CWR were identified as those in gene pools or provisional gene pools 1B and 2 (closely related CWR from which gene transfer to the crop is possible and does not require sophisticated techniques) or taxon groups 1B–3 (CWR within the same subgenus as the crop). In addition to those priority taxa identified within the prioritisation concepts, more distantly related taxa that are documented to have been previously used for crop improvement or which have shown promise for crop improvement were also given priority status, many of which having recently been identified by Maxted and Kell (2009).

Gene pool concepts were obtained from a literature review of published concepts. Taxon group concepts were derived from published taxonomic classifications (primarily phylogenetic taxonomy) for crops where no gene pool concept could be found. A provisional recommendation for which GP, TG or PGP concept was to be used for each crop complex was proposed by the project team, then a panel of experts with specialist knowledge of each crop complex was consulted and agreement reached over which concept should be applied within the inventory.

Table 2.2 Prioritisation concepts used in the creation of the global priority crop wild relative (CWR) list

Prioritisation concept	**Sublevel description**	**Prioritisation concept description**
Gene pool	GP1A: cultivated crop taxa	Based upon the Harlan and de Wet gene pool concept (1971), experts assign each CWR to the appropriate
	GP1B: (primary GP): wild or weedy forms of the crop that cross easily with the crop	

	GP2 (secondary GP): less closely related species from which gene transfer to the crop is possible but difficult using conventional breeding techniques	sublevel based upon crossability data. The highest priority CWR are those in GP1B and GP2, which can be most easily crossed with the crop.
	GP3 (tertiary GP): species from which gene transfer to the crop is impossible, or if possible, requires sophisticated techniques, such as embryo rescue, somatic fusion or genetic engineering	
Taxon group	TG1A: cultivated crop taxa	The taxon group concept employs taxonomic hierarchy as a proxy for taxon genetic relatedness and thus crossability (Maxted *et al.*, 2006). The highest priority CWR are those in TG1B, TG2 and TG3, which can be most easily crossed with the crop.
	TG1B: taxa within the same species as the crop	
	TG2: taxa within the same series or section as the crop	
	TG3: taxa within the same subgenus as the crop	
	TG4: taxa within the same genus as the crop	
	TG5: taxa within the same tribe as the crop	
Provisional gene pool	PGP1A: cultivated crop taxa	This concept is used where there is no formally published gene pool concept and where taxonomic treatments lack subgeneric information, but where some crossability evidence between the crop and related taxa was available. This approach is the least favoured as it lacked the
	PGP1B: (primary PGP): wild or weedy forms of the crop that cross easily with the crop	
	PGP2 (secondary PGP): less closely related species from which gene transfer to the crop is possible but difficult using conventional breeding techniques	
	PGP3 (tertiary PGP): species from	

	which gene transfer to the crop is impossible, or if possible, requires sophisticated techniques, such as embryo rescue, somatic fusion or genetic engineering	expert input that exists in published gene pool concepts and taxonomic treatments.

To manage the CWR data, a web-enabled extendable database was designed which will allow revision and addition as crop/ CWR crossability and relatedness data become available and permit interaction with other databases. Once the taxonomic backbone was entered into the database, other data were added for each taxon, including common synonyms and vernacular names, prioritisation concepts, countries of occurrence, actual and potential use in plant breeding, other direct uses, seed storage behaviour, and the main herbaria where specimens are expected to be stored (derived from geographical distribution of the taxon). These additional data were compiled from various sources, including literature surveys, online databases (ILDIS, 2011; Tropicos, 2011; USDA, 2011) and the Seed Information Database (Royal Botanic Gardens Kew, 2008). The Plant List (Royal Botanic Gardens Kew, 2011) was used as the nomenclature standard. The database was then made available to crop specific experts to provide feedback and to ensure that the CWR inventory was as accurate as possible. Following review, the database was revised and made available to all users online at http://www.cwrdiversity.org/checklist/. The inventory is named the ‘Harlan and de Wet CWR Inventory’ in honour of the scientists who originally proposed the crop gene pool concept (Harlan and de Wet, 1971).

2.3.2 Analysis of the Harlan and de Wet inventory

The GIS program DIVA-GIS (Hijmans *et al.*, 2005) was used to visualise the richness of CWR taxa at species level per country, per geographic region of the world using the TDWG standard (Brummitt, 2001) and per Vavilov centre of diversity (Vavilov, 1935). The Vavilov centres of diversity are geographical areas where domestication of important food crops is thought to have taken place and where the genetic diversity of these crop complexes is still thought to be concentrated. By discovering which countries, regions and centres are the richest in terms of priority CWR, we can more efficiently plan conservation efforts to target them. To gain an insight into the effectiveness of current *ex situ* conservation efforts for the priority CWR taxa, *ex situ* holdings data were extracted from the Global Biodiversity Information Facility (GBIF, 2013) and reviewed. Botanical garden records for CWR that have non-orthodox seeds (i.e., seeds that cannot be conserved using conventional drying and freezing techniques) were also included in this analysis.

2.4 Results

The inventory contains 1667 priority CWR taxa in 173 crop complexes (see Supplementary Table 2.1), 37 families, 108 genera, 1392 species and 299 sub-specific taxa. Families and genera are listed in Table 2.3 along with the corresponding numbers of priority CWR taxa. The family with the most CWR is Leguminosae (Fabaceae) (253), followed by Rosaceae (194), Poaceae (150), Solanaceae (131) and Rubiaceae (116); while the genera with the most CWR are *Solanum* (124), *Coffea* (116), *Prunus* (102), *Ficus* (59) and *Ribes* (53). Of the 173 crop complexes included, 88 are prioritised using published gene pool concepts, 15 using provisional gene pool concepts and 71 using taxon group concepts. The taxon group concept was applied to a further 16 crop gene pools for which there is no detailed subgeneric classification so in these cases, all taxa in the genus were included. These are the gene pools of: *Agropyron cristatum**, *Elaeis oleifera*, *Armoracia rusticana*, *Elettaria cardamomum*, *Barbarea verna*, *Ensete ventricosum*, *Carica papaya**, *Phoenix dactylifera*, *Colocasia esculenta, Pimenta dioica*, *Digitaria exilis*, *Rorippa indica*, *Echinochloa frumentacea*, *Sesamum indicum*, *Elaeis guineensis** and *Xanthosoma sagittifolium* (those marked with * are crops that are documented to have been improved using CWR material).

Table 2.3 Global priority crop wild relative (CWR) numbers per family and genus.

Family	**Number of CWR**	**Genus**	**Number of CWR**
Amaranthaceae	42	*Beta*	13
		Chenopodium	27
		Spinacia	2
Amaryllidaceae	35	*Allium*	35
Anacardiaceae	61	*Mangifera*	46
		Pistacia	15
Apiaceae	21	*Daucus*	18
		Tornabenea	3
Aquifoliaceae	36	*Ilex*	36
Araceae	2	*Colocasia*	1
		Xanthosoma	1
Arecaceae	4	*Cocos*	1
		Elaeis	2
		Phoenix	1
Asparagaceae	18	*Asparagus*	18
Betulaceae	15	*Corylus*	15

Brassicaceae	70	*Armoracia*	1
		Barbarea	1
		Brassica	28
		Capsella	1
		Coincya	1
		Crambe	2
		Diplotaxis	3
		Eruca	3
		Erucastrum	2
		Isatis	4
		Lepidium	12
		Moricandia	1
		Orychophragmus	1
		Raphanus	5
		Rorippa	1
		Sinapis	3
		Trachystoma	1
Bromeliaceae	5	*Ananas*	5
Caricaceae	4	*Carica*	1
		Vasconcellea	3
Compositae	70	*Carthamus*	10
		Cynara	5
		Helianthus	44
		Lactuca	11
Convolvulaceae	14	*Ipomoea*	14
Cucurbitaceae	48	*Citrullus*	3
		Cucumis	34
		Cucurbita	11
Dioscoreaceae	15	*Dioscorea*	15

Euphorbiaceae	28	*Manihot*	28
Grossulariaceae	53	*Ribes*	53
Juglandaceae	30	*Juglans*	30
Lauraceae	7	*Persea*	7
Lecythidaceae	1	*Bertholletia*	1
Leguminosae	253	*Arachis*	16
		Cajanus	14
		Cicer	5
		Glycine	5
		Lablab	3
		Lathyrus	34
		Lens	4
		Lupinus	29
		Medicago	26
		Phaseolus	36
		Pisum	6
		Vicia	33
		Vigna	42
Malvaceae	29	*Gossypium*	26
		Theobroma	3
Moraceae	71	*Artocarpus*	12
		Ficus	59
Musaceae	46	*Ensete*	1
		Musa	45
Myrtaceae	1	*Pimenta*	1
Oleaceae	8	*Olea*	8
Pedaliaceae	8	*Sesamum*	8
Piperaceae	7	*Piper*	7
Poaceae	150	*Aegilops*	32

		Agropyron	2
		Amblyopyrum	3
		Avena	15
		Digitaria	1
		Echinochloa	1
		Eleusine	7
		Elymus	5
		Hordeum	4
		Oryza	23
		Panicum	8
		Pennisetum	5
		Saccharum	11
		Secale	7
		Setaria	4
		Sorghum	6
		Tripsacum	1
		Triticum	8
		Zea	7
Rosaceae	194	*Amygdalus*	1
		Cydonia	1
		Fragaria	15
		Malus	38
		Potentilla	1
		Prunus	102
		Pyrus	36
Rubiaceae	116	*Coffea*	116
Rutaceae	18	*Atalantia*	1
		Citrus	16
		Clausena	1

Solanaceae	131	*Capsicum*	7
		Solanum	124
Theaceae	34	*Camellia*	34
Vitaceae	21	*Vitis*	21
Zingiberaceae	1	*Elettaria*	1

The global priority CWR taxa are native to 39 world regions (Figure 2.1). The region with the most CWR taxa present is western Asia with 262, second is China with 222 and third is southeastern Europe with 181. There are 203 countries that have at least one native global priority CWR taxon (see Supplementary Table 2.2). China has the highest number with 222 taxa, Turkey has 189, the USA has 152, Italy has 139 and Greece has 134. The CWR most likely to be used by breeders are either in GP1B, PGP1B or TG1B, which are the closest wild relatives to the crop where there are no hybridisation barriers. The countries with the highest number of native CWR in GP1B, PGP1B or TG1B are Turkey with 86, Greece with 71, Spain with 66, Italy and Iran with 63 and France with 60. However, the number of CWR per country does not take into account the size of the country, so care should be taken when drawing conclusions about these countries being CWR hotspots. If all countries with over 80 priority CWR are recalculated to indicate the unit area per CWR, then the countries with the highest concentration of all priority CWR are Lebanon, Israel, Greece, Portugal, Azerbaijan, Bulgaria, Syria, Italy, Spain and Turkey (Table 2.4). But in absolute terms the countries with the highest concentration of CWR per unit area are all small islands which are likely to contain higher numbers of endemic taxa but whose CWR numbers tend to be inflated by invasive, weedy CWR. Species richness per country was further adjusted to reflect the species-area-relation pattern (Table 2.4), by dividing species richness by A^z where A is the country area and z is a typical value for the slope of a nested plot of log(species richness) on log(country area), set here as 0.25 (Rosenzweig, 1995; Smith *et al.,* 2003). The most species rich countries adjusted for country area were: Lebanon, Israel, Greece, Turkey, Albania, Armenia, Italy, Syria, Azerbaijan and Bulgaria.

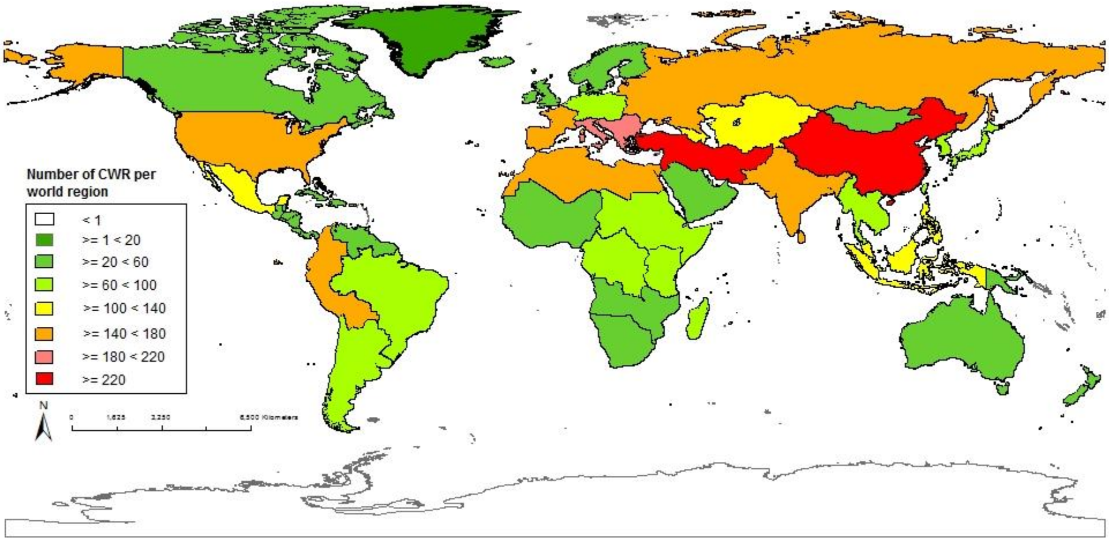

Figure 2.1 Number of priority crop wild relatives (CWR) per world region.

Table 2.4 Concentration and numbers of crop wild relatives (CWR) per country, where total priority CWR is above 80. TG = Taxon Group Concept, GP = Gene Pool Concept, PGP = Provisional Gene Pool Concept.

Country	**TG 1A**	**TG 1B**	**TG 2**	**TG 3**	**GP 1B**	**GP 2**	**PGP 1B**	**PGP 2**	**Priority CWR**	**Country Area (km^2)**	**Unit area per CWR**	**Adjusted CWR richness for country area**
Lebanon	9	0	24	4	17	34	1	1	97	10 452	108	9.59
Israel	7	0	24	6	18	30	1	2	98	22 072	225	8.04
Albania	8	0	18	6	17	20	0	1	81	28 748	355	6.22
Armenia	10	1	11	5	20	22	0	0	81	29 743	367	6.17
Azerbaijan	9	1	17	5	22	27	0	0	91	86 600	952	5.30
Greece	13	0	28	9	28	33	1	1	134	131 957	985	7.03
Portugal	10	0	19	5	19	16	0	3	91	92 090	1 012	5.22
Bulgaria	11	0	22	8	20	24	0	0	96	110 879	1 155	5.26
Syria	9	0	28	6	17	41	1	1	112	185 180	1 653	5.40
Italy	17	0	30	8	25	32	0	1	139	301 336	2 168	5.93
Spain	16	0	26	7	22	32	0	3	132	505 992	3 833	4.95
Turkey	17	1	43	8	40	55	1	1	189	783 562	4 146	6.35
Morocco	8	0	18	6	12	27	2	1	99	446 550	4 511	3.83
Iraq	8	1	18	5	22	28	0	0	90	435 244	4 836	3.50
France	15	0	23	6	22	22	0	1	111	640 294	5 768	3.92
Ukraine	11	0	14	8	19	22	0	0	86	603 500	7 017	3.09
Iran	13	1	24	9	36	37	0	0	131	1 648 195	12 582	3.66
Peru	7	0	2	3	16	56	4	3	96	1 285 216	13 388	2.85
Mexico	4	0	9	7	14	55	0	8	109	1 964 375	18 022	2.91
Indonesia	4	0	27	38	6	7	1	0	84	1 910 931	22 749	2.26

Algeria	9	0	19	4	16	24	1	1	96	2 381 741	24 810	2.44
India	9	0	23	19	17	30	6	0	123	3 287 263	26 726	2.89
China	11	1	75	21	25	59	0	0	221	9 640 011	43 620	3.97
USA	3	0	46	16	8	41	0	7	152	9 629 091	63 349	2.73
Russia	12	1	38	11	20	26	0	0	117	17 075 200	145 942	1.82

The inventory contains 526 CWR taxa that have a confirmed or documented potential use in crop breeding. ‘Confirmed use’ means that gene transfer from the CWR to the crop has been successful, while ‘potential use’ is recorded for CWR taxa that have been found to have important genes or traits for crop improvement, but where breeding has not been totally successful or yet attempted because more sophisticated techniques are required. *Prunus* has the most CWR taxa used in breeding or with breeding potential (68), which is partially due to the large number of CWR taxa that are used in grafting as rootstocks (e.g. *P. persica*, *P. davidiana, P. cerasifera* and *P. dulcis*). This is followed by *Solanum* with 32 CWR used in crop breeding (e.g. *S. acaule, S. chacoense, S. spegazzinii* and *S. vernei*). Note that both genera are large in terms of numbers of taxa included and contain multiple crops, thus boosting the number of CWR. Analysing the inventory in terms of breeding use, the majority of CWR taxa (240) have been used in disease resistance breeding, whilst 170 have been used as graft stock and 103 used in pest resistance breeding.

Brown and Marshall (1995) propose that a minimum of 50 sites are sampled to adequately conserve the genetic diversity of a taxon *ex situ*. Of the 1667 priority CWR taxa included in the inventory, there are 1247 taxa with 50 or less *ex situ* accessions (see Supplementary Table 2.1) and of these, 939 taxa have 10 or fewer accessions and 542 have no accessions at all. What is particularly concerning is that 242 of the 422 primary level (GP1B, PGP1B and TG1B) taxa were found to be represented by fewer than 50 *ex situ* accessions in gene banks (see Supplementary Table 2.3). The ten most important countries for further collecting of under-represented primary level taxa are: China, Mexico, Brazil, USA, Iran, Turkey, Spain, Greece, Indonesia and Guatemala. Of these, China, Mexico and Brazil have 143, 95 and 54 native priority primary level taxa respectively. Table 2.5 lists the total number of CWR taxa per crop prioritisation concept and the percentage of these that have fewer than 50 accessions stored *ex situ*. The results indicate that all of the priority CWR of 18 crops are represented by fewer than 50 *ex situ* germplasm accessions, including onion, pineapple, spinach and coconut, and that 80% of the priority CWR of a further 49 crops have fewer than 50 accessions stored *ex situ*. It should also be noted that a high level of duplicated accessions between genebanks was noted which would tend to, if anything, over emphasise the actual *ex situ* conservation status of individual CWR. While acknowledging that the data accessible via GBIF may not be complete, it does suggest that the majority of priority CWR taxa are not currently adequately conserved *ex situ*.

Table 2.5 Number of priority crop wild relatives (CWR) per crop and the percentage with less than 50 accessions stored ex situ.

Scientific name	**Common name**	**Number of priority CWR**	**Percentage of priority CWR with less than 50 *ex situ* accessions**
Agropyron cristatum	Crested wheatgrass	2	0
Allium cepa	Onion	3	100
Allium sativum	Garlic	1	0
Allium chinense	Chinese scallion	23	91
Allium tuberosum	Chinese chives	2	50
Allium schoenoprasum	Chives	23	91
Allium fistulosum	Welsh Onion	5	60
Allium porrum	Leek	8	75
Ananas comosus	Pineapple	5	100
Arachis hypogaea	Peanut	16	94
Armoracia rusticana	Horseradish	1	0
Artocarpus altilis	Breadfruit	12	92

Artocarpus heterophyllus	Jackfruit	12	92
Asparagus officinalis	Asparagus	18	94
Avena sativa	Oat	15	60
Barbarea verna	American cress	1	100
Bertholletia excelsa	Brazil nut	1	100
Beta vulgaris	Sugarbeet	13	54
Brassica juncea	Mustard	9	22
Brassica napus	Rape	24	54
Brassica rapa	Turnip	19	58
Brassica oleracea	Kale	25	72
Brassica carinata	Ethiopian cabbage	3	0
Brassica nigra	Black mustard	7	14
Cajanus cajan	Pigeonpea	14	86
Camellia sinensis	Tea	34	94
Capsicum annuum	Bell pepper	5	20
Capsicum baccatum	Aji	5	40
Capsicum chinense	Bonnet pepper	5	20
Capsicum frutescens	Red chili	5	20
Carica papaya	Papaya	4	75
Carthamus tinctorius	Safflower	10	90
Chenopodium quinoa	Quinoa	27	93
Cicer arietinum	Chickpea	5	20
Citrullus lanatus	Watermelon	3	0
Citrus aurantiifolia	Key lime	13	54
Citrus limon	Lemon	12	50
Citrus sinensis	Sweet orange	16	63
Citrus aurantium	Sour orange	13	54
Citrus paradisi	Grapefruit	12	50
Citrus limetta	Sweet lime	12	50
Citrus reticulata	Mandarin	13	46
Cocos nucifera	Coconut	1	100

Coffea arabica	Arabic coffee	116	99
Coffea canephora	Robusta coffee	116	99
Colocasia esculenta	Taro	1	100
Corylus maxima	Giant filbert	15	60
Corylus avellana	Hazelnut	11	45
Crambe hispanica	Ethiopian kale	2	100
Cucumis sativus	Cucumber	3	33
Cucumis melo	Melon	32	78
Cucurbita ficifolia	Blackseed squash	2	100
Cucurbita pepo	Acorn squash	7	57
Cucurbita argyrosperma	Cushaw	1	0
Cucurbita moschata	Butternut squash	0	0
Cucurbita maxima	Pumpkin	3	67
Cynara cardunculus	Artichoke	5	80
Daucus carota	Carrot	21	95
Digitaria exilis	Fonio millet	1	100
Dioscorea alata	Water yam	8	63
Dioscorea cayennensis	Lagos yam	7	71
Dioscorea bulbifera	Aerial yam	1	0
Dioscorea esculenta	Asiatic yam	1	100
Dioscorea dumetorum	Bitter yam	1	0
Dioscorea rotundata	White Guinea yam	4	50
Diplotaxis tenuifolia	Perennial wall rocket	5	20
Echinochloa frumentacea	White millet	1	0
Elaeis guineensis	African oil palm	2	50
Elaeis oleifera	American oil palm	2	50
Elettaria cardamomum	Cardamom	1	0
Eleusine coracana	Finger millet	7	86
Elymus hispidus	Intermediate wheatgrass	5	40

Ensete ventricosum	Ethiopian banana	1	100
Eruca versicaria	Salad rocket	7	29
Ficus carica	Fig	59	98
Fragaria × ananassa	Strawberry	16	63
Glycine max	Soybean	5	20
Gossypium hirsutum	Cotton	26	69
Gossypium arboreum	Tree cotton	26	69
Gossypium barbadense	Sea Island cotton	26	69
Gossypium herbaceum	Short-staple cotton	26	69
Helianthus annuus	Sunflower	38	76
Helianthus tuberosus	Jerusalem artichoke	15	60
Hordeum vulgare	Barley	4	0
Ilex paraguariensis	Yerbe maté	36	100
Ipomoea batatas	Sweet potato	14	57
Isatis tinctoria	Woad	4	75
Juglans nigra	Black walnut	14	79
Juglans regia	English walnut	29	86
Juglans ailantifolia	Japanese walnut	6	33
Lablab purpureus	Hyacinth bean	3	67
Lactuca sativa	Lettuce	11	73
Lathyrus cicera	Chickling vetch	30	63
Lathyrus ochrus	Cyprus vetch	3	33
Lathyrus odoratus	Sweetpea	29	66
Lathyrus sativus	Grass pea	4	50
Lens culinaris	Lentil	4	0
Lepidium meyenii	Maca	11	91
Lepidium sativum	Garden cress	1	0
Lupinus albus	White lupin	4	25
Lupinus luteus	Yellow lupin	6	50
Lupinus cosentinii	Sandplain lupin	7	71

Lupinus mutabilis	Andean lupin	15	73
Lupinus angustifolius	Blue lupin	6	50
Malus domestica	Apple	38	55
Mangifera indica	Mango	46	98
Manihot esculenta	Cassava	28	82
Medicago sativa	Alfalfa	15	60
Medicago truncatula	Barrel medic	11	18
Musa acuminata	Banana	40	95
Musa balbisiana	Plantain	40	95
Musa textilis	Manila hemp	6	100
Olea europaea	Olive	8	75
Oryza glaberrima	African rice	23	52
Oryza sativa	Rice	23	52
Panicum miliaceum	Broom millet	8	75
Pennisetum glaucum	Pearl millet	5	40
Persea americana	Avocado	7	86
Phaseolus vulgaris	Common bean	6	50
Phaseolus dumosus	Year bean	3	33
Phaseolus acutifolius	Tepary bean	3	33
Phaseolus lunatus	Lima bean	5	60
Phaseolus coccineus	Scarlet runner bean	25	80
Phoenix dactylifera	Date palm	1	0
Pimenta dioica	Pimenta	1	100
Piper nigrum	Black pepper	7	86
Pistacia vera	Pistachio	15	80
Pisum sativum	Pea	8	38
Prunus avium	Sweet cherry	27	74
Prunus armeniaca	Apricot	15	53
Prunus cerasifera	Myrobalan plum	13	62
Prunus cerasus	Sour cherry	10	50
Prunus domestica	Plum	21	62

Prunus dulcis	Almond	32	78
Prunus persica	Peach	28	64
Prunus salicina	Japanese plum	27	74
Pyrus communis	Pear	32	72
Pyrus pyrifolia	Asian pear	18	72
Raphanus sativus	Radish	5	20
Ribes nigrum	Blackcurrant	19	84
Ribes rubrum	Redcurrant	15	93
Ribes uva-crispa	Gooseberry	22	96
Rorippa indica	Variableleaf yellowcress	1	100
Saccharum officinarum	Sugarcane	11	72
Secale cereale	Rye	7	57
Sesamum indicum	Sesame seed	8	88
Setaria italica	Foxtail millet	4	75
Sinapis alba	White mustard	2	50
Solanum lycopersicum	Tomato	12	42
Solanum melongena	Aubergine	18	78
Solanum muricatum	Pepino	6	100
Solanum tuberosum	Potato	88	55
Sorghum bicolor	Sorghum	6	50
Spinacia oleracea	Spinach	2	100
Theobroma cacao	Cacao	3	67
Triticum aestivum	Wheat	47	28
Vicia articulata	Monantha vetch	2	0
Vicia ervilia	Bitter vetch	2	0
Vicia faba	Faba bean	0	0
Vicia narbonensis	Narbon bean	6	67
Vicia pannonica	Hungarian vetch	12	67
Vicia sativa	Common vetch	9	56
Vigna angularis	Adzuki bean	13	77

Vigna mungo	Black gram	21	71
Vigna radiata	Mung bean	24	67
Vigna subterranea	Bambara groundnut	2	100
Vigna umbellata	Rice bean	23	70
Vigna unguiculata	Cowpea	14	86
Vitis amurensis	Amur grape	1	0
Vitis rotundifolia	Muscadine grape	2	0
Vitis vinifera	Wine grape	20	60
Xanthosoma sagittifolium	New cocoyam/Tania	1	0
Zea mays	Maize	8	63

The distributions of the taxa in the inventory were compared to the Vavilov centres of diversity. As the data on geographical distribution are mostly specified at the country level within the inventory, whole countries were used to represent each Vavilov centre. Figure 2.2 shows that the Vavilov centres richest in priority CWR are the Chinese centre (centre 1) with 262 native CWR taxa and the Near Eastern centre (centre 4) with 254, representing 15.7% and 15.2% of the total global priority CWR respectively. In total, there are 1,053 CWR found in Vavilov centres, representing 63% of the priority CWR of major and minor crops of the world.

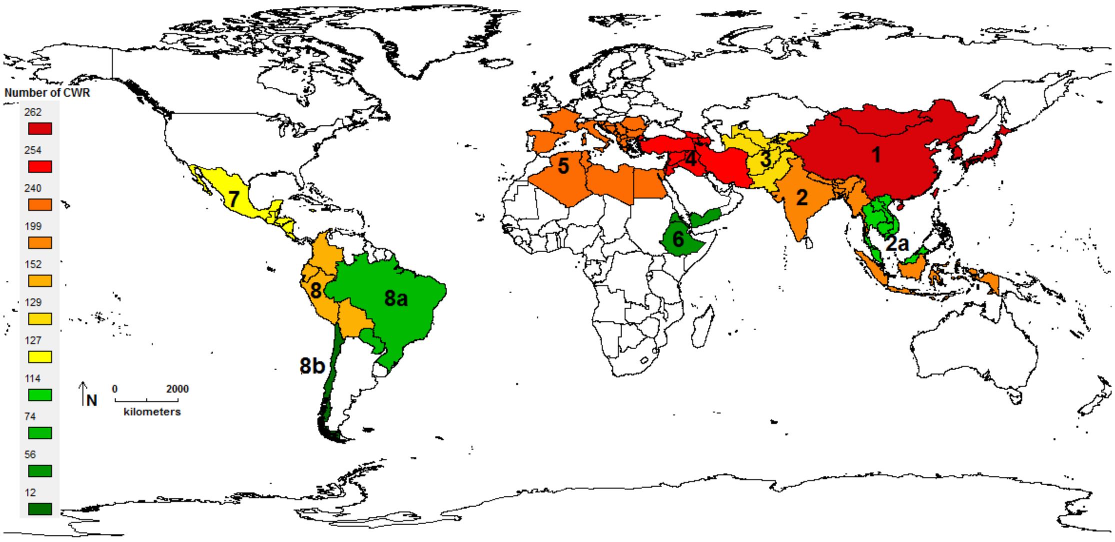

Figure 2.2 Number of priority crop wild relatives (CWR) per Vavilov Centre of Diversity.

Table 2.6 ranks the ten most important crops in the world in terms of global net production value according to FAOSTAT (2012) along with the number of priority CWR per crop. With 24 CWR, the rice gene pool has the highest economic value per CWR and apple the lowest economic value per CWR with 31. Potato is ranked 6th in production value but has the highest number of CWR (75), while soybean is economically ranked 3rd but has only one priority CWR. The CWR of these economically important crops were analysed at the species level to identify the most species rich countries. The country with the most native CWR species is Peru with 58, followed by Mexico (39), China (35), Turkey (26) and Bolivia (23).

Table 2.6 The ten most important crops in the world in terms of global net production value according to FAOSTAT (FAOSTAT, 2012) with numbers of priority CWR per crop.

Crop	**Global net production value (1,000 Int. $ at the constant 2004–2006 rate)**	**Number of priority CWR**
Rice	178 343 133	24
Wheat	86 720 367	44
Soybean	57 587 844	1

Tomato	55 894 436	12
Sugar cane	52 496 605	12
Maize	51 157 146	7
Potato	44 128 413	75
Grape	38 616 843	6
Cotton	29 936 716	29
Apple	29 919 202	31

Information on seed storage behaviour was collated for species from all 108 priority CWR genera in the inventory. Storage behaviour for each genus is recorded as the percentage of CWR that exhibit that behaviour within the genus. The four behaviour categories are orthodox (seed which will survive standard drying and freezing techniques), intermediate (seed that tolerates some drying, but is between orthodox and recalcitrant in behaviour), recalcitrant (seed that cannot withstand standard drying and freezing and cannot be stored for long periods), and unknown. For this analysis, the category assigned to at least 70% of the total species within a genus was accepted as the storage behaviour of the genus. Of the 108 genera in the inventory, 5.5% (6) are recalcitrant, 8.3% (9) are intermediate, 75.2% (82) are orthodox and 11% are unknown. An understanding of *ex situ* seed storage behaviour is vital for conservation planning to ensure survival of the seed via the appropriate storage method, and since the majority have orthodox seeds there is no technical reason why they should not be conserved systematically *ex situ*.

2.5 Discussion

The Harlan and de Wet CWR Inventory is available at www.cwrdiversity.org/checklist/. The inventory is the first annotated list of priority CWR of the world's most important human and animal food crops. It is already proving to be a significant resource for conservation planning either at the geographic (global, regional and national), or crop complex and multiple crop complex levels. For example, it was used for global ecogeographic studies of the barley (Vincent *et al.*, 2012) and grasspea (Shehadeh *et al.*, 2013) gene pools, and for producing a national CWR inventory for the USA (Khoury *et al.*, 2013). Further national CWR conservation strategy planning utilising data from the Harlan and de Wet Inventory is underway in Spain, Libya, Jordan and a number of other countries in Europe. The inventory also provides the foundations for the 'Adapting agriculture to climate change: collecting, protecting and preparing crop wild relatives' project (GCDT, 2011), which aims to systematically conserve *ex situ* the CWR diversity most likely to be of use in underpinning global food security and to use the conserved CWR diversity in novel breeding for crop improvement. The inventory is also being used to inform the planning of the establishment of a global network for *in situ* CWR conservation (FAO, 2013). Already including 173 crops and their related 1667 priority CWR taxa, the Harlan and de Wet inventory is comprehensive, but in future the inventory will be expanded to include further crop complexes. The inventory will also have the capacity to include more than one prioritisation concept (i.e. gene pool, taxon group or provisional gene pool) per crop. The importance of this can be explained with the example of *Citrus*. Swingle and Reece (1943) recognise 16 species, whereas Tanaka (1977) recognises 162; therefore the online inventory should be able to include multiple prioritisation concepts per crop, allowing users to choose a concept or make one aggregated concept from all that are available. Thus, the inventory will act as a global repository for prioritisation concepts and will be conceptually and taxonomically neutral as no particular concept will be seen as the preferred concept and problems of disagreements between experts can be avoided.

The geographic analysis of native priority CWR highlighted that south-central Asia is the region with the highest number of taxa, followed by eastern and western Asia. The eastern, south-central and western Asia areas were also highlighted as the most important for priority CWR when the Vavilov centres of diversity concept was applied. This is possibly due to the high number of minor crops originating in the eastern and south-central Asia regions that have no gene pool concept and where the taxon group concept has been applied. For example, tea (*Camellia sinensis*) has 32 priority CWR based on the taxon group concept, which is relatively high compared to most gene pool concepts. It is not known if all of these CWR are actually important in tea breeding, so it may potentially lead to an inflated number of priority CWR present in these regions. Furthermore, these regions have relatively high numbers of fruit trees such as *Prunus*, *Malus*, *Pyrus* and *Ficus* species. Large numbers of these taxa are used in grafting as well as breeding so they are included in the inventory, but their inclusion substantially increases the number of priority CWR found in these regions. Not surprisingly, the major crop complexes and their related CWR have been studied more extensively by the scientific community so the number of priority CWR tends to be fewer because the distinction between close and more distant CWR has been more firmly established (e.g. *Hordeum* – Bothmer *et al.*, 1995; *Pisum* – Maxted and Ambrose, 2001; *Cicer* – Ahmad *et al.*, 2005; *Lens* – Muehlbauer and McPhee, 2005). The number of CWR per region or country may be somewhat misleading as regions and countries vary considerably in size, so perhaps a more useful view of geographic priorities can be obtained from the unit area per CWR within a country. The countries with the highest CWR concentration per unit area are: Lebanon, Israel, Greece, Portugal, Azerbaijan, Bulgaria, Syria, Italy, Spain and Turkey; six of which are from the Fertile Crescent (Lebanon, Israel, Greece, Azerbaijan, Syria and Turkey) and four from southern Europe (Portugal, Bulgaria, Italy and Spain). Even this does not take into account the distribution of CWR within each country. For example, CWR are found throughout Lebanon and Azerbaijan, but in Greece and Turkey they tend to be concentrated in the south and east, in Israel in the north and in Syria in the western Jebel Al Nusayriyah. In the latter case this is an area of less than 5% of the total area of Syria — an area already indicated to be key for cereal and legume CWR conservation (Maxted *et al.*, 2012a).

The literature concerning breeders' use of CWR diversity is growing rapidly (Maxted *et al.*, 2012b). It is important to note that in this initial version of the inventory the citation for CWR use is not exhaustive—there are likely to be CWR which have been used in crop improvement successfully or have great use potential that are not included, but these will be added as they are identified, further enhancing the resource for the user community. The numbers of high priority CWR with fewer than 50 accessions highlighted in Supplementary Table 2.1 is a matter of concern— if CWR remain unconserved *ex situ* they are unlikely to be used (Maxted and Kell, 2009). Further, a high level of duplicated accessions between genebanks was noted which might also give a false impression of actual taxon conservation *ex situ*. Both factors lead us to suggest that the level of genetic diversity actually conserved could be much lower than originally thought. However, it should be noted that GBIF does not hold data on all existing *ex situ* accessions of priority CWR stored in gene banks, so the actual number of accessions may not be as low as portrayed here. Nonethless, the values provided here do act as a preliminary estimate of *ex situ* conservation effectiveness and are comparable with a similar analysis of priority CWR held *ex situ* in Europe (Kell *et al.*, 2012). Futhermore, it is important to note that many existing genebank accessions are only recorded at the species level which may explain the low numbers of *ex situ* records for subspecific taxa found in Supplementary Table 2.1. Therefore it is vital for anyone planning conservation of CWR to consult individual genebanks for a more accurate understanding of current conservation efforts before any action is undertaken. Given that 75% of priority CWR taxa were found to be orthodox in terms of their seed storage behaviour it bodes well for the GCDT (2011) project being able to significantly improve this position in the coming years. Just as the identification of Biodiversity hotspots has facilitated the targeting of conservation action, particularly highlighting the need for more active conservation or restoration in hotspots threatened by habitat destruction (Mittermeier *et al.*, 2004), so we hope that a clearer understanding of the presence and numbers of CWR in individual countries, regions or Vavilov centres of diversity will help promote targeted conservation action. Further, it is also clear that not all Vavilov centres have equal value in terms of the numbers of priority CWR present; for example, there are significant differences between the Chinese centre with 262 and the Chilean centre with 12. However, having made this comparison it is important to understand that numbers of CWR alone are likely to provide relatively crude means of targeting CWR conservation action; the value of the related crop itself should also be considered and high priority CWR taxa may also be found outside of the Vavilov centres. However, it is interesting to note the general agreement between the current distributional analysis and the Vavilov centres as proposed almost a century ago (Vavilov, 1926).

To conclude, the Harlan and de Wet CWR inventory provides a resource that will inform future CWR conservation and use, thus underpinning efforts to adapt agriculture to the environmental challenges related to climate change. The first global list of priority CWR species containing 1,667 taxa (1,392 species and 299 subspecific taxa) is already making a significant contribution to targeted conservation action. The inventory is currently being used as a resource for CWR prioritisation in several projects other than the Global Crop Diversity

Trust project for which it was originally developed, including the creation of national CWR inventories for Wales, Spain, Libya and Jordan, and a regional conservation strategy for Europe. Now that we know which taxa are of highest importance, it will be possible to plan and implement an effective worldwide *in situ* and *ex situ* conservation strategy for this critical global resource. The next step will be to collate georeferenced data points for the priority CWR and compare their distributions with existing *in situ* and *ex situ* conservation actions to identify priority areas for further *in situ* conservation activities and *ex situ* collection. Plant breeders cannot breed climate change resilient varieties without access to the full range of conserved CWR diversity and more effective CWR use is likely to provide sustainability to conservation actions; as such the Harlan and de Wet CWR inventory will underpin both future CWR conservation and utilisation activities.

CHAPTER 3

Global priorities for *in situ* conservation of wild plant genetic resources: towards the establishment of a global network of crop wild relative reserves

This chapter is being prepared for publication as:

Vincent, H., Castañeda-Álvarez, N.P.and Maxted, N. (2016) Global priorities for *in situ* conservation of wild plant genetic resources: towards the establishment of a global network of crop wild relative reserves (in prep.)

Author contributions:

Conceived and designed the study: **HV**, NM

Data collation and preparation: **HV**, NPCA

Performed analysis: **HV**

Analysed results: **HV**

Wrote the paper: **HV**

Critically reviewed the paper: **HV**, NM

3.1 Abstract

The combined effects of climate change and the projected rise in human global population is likely to push current agricultural systems to crisis point by 2050, if not sooner. Crop wild relatives (CWR), the wild cousins of cultivated crops, are a vast, underutilised source of genetic diversity which can assist in breeding new higher yielding, climate change tolerant crop varieties. However, CWR are threatened in the wild and are massively under conserved, particularly *in situ.*To improve knowledge on the state of current CWR *in situ* protection and formulate strategies for their improved conservation, a global *in situ* gap analysis was undertaken for 1261 priority CWR and their genetic diversity – estimated by environmental niche. Results indicate that the majority of CWR are passively conserved across the existing protected area network; however, 85 species are projected to lose over 50% of their current predicted range by 2070. To improve *in situ* CWR conservation worldwide in and outside protected areas, 150 priority sites covering 829 CWR are suggested for reserve establishment, maximising species and genetic diversity representation, whilst mitigating for distribution losses under future climates.

3.2 Introduction

Ensuring global food security now and for the future is perhaps the greatest challenge of our time. Currently 1 in 9 people worldwide suffer from chronic hunger (FAO, IFAD and WFP, 2015) and with the human population projected to rise to 9.7 billion by 2050 (United Nations, 2015), the pressure on the food production chain is likely to increase dramatically (Godfray *et al.*, 2010; Porter *et al.*, 2014). In fact, it is estimated that food supplies in developing countries will need to increase by 100%, with a 60% increase globally by 2050 (FAO, 2011b) to meet this growing demand. Food security is also expected to be greatly impacted by the effects of climate change. The Intergovernmental Panel on Climate Change (IPCC) fifth assessment predicts that crop yield losses are projected to rise to up to 25% in the latter half of the century if crop varieties are not adapted to changing climates (Challinor *et al.*, 2014; IPCC, 2014). In addition to the dual deleterious impact of climate change and an increased population upon food security, other pressures such as diminishing water supplies, dwindling natural resources and competition for land, emphasise the urgent need for smarter, more efficient agricultural systems. Whilst improvements in current food security could be made by changing social behaviours such as altering diets and preventing unnecessary food waste (Godfray *et al.*, 2010; Parfitt *et al.,* 2010), the threat of climate change is more difficult to mitigate. One potential solution is the production of a new generation of crop varieties that utilise a wider range of genetic diversity that can better withstand the extremes of climate change, endure exposure to pests and diseases, require fewer resources for growth and provide a greater concentration of nutritional benefits (McCouch *et al.*, 2013; IPCC, 2014).

Crop wild relatives (CWR); wild and weedy plants closely related to cultivated crops, are a rich and underutilised source of novel genetic diversity for crop breeding (Maxted and Kell, 2009). As wild species, CWR have not passed through a genetic bottleneck of domestication, and thus retain a wider breadth of genetic diversity than their related crops (Tanksley and McCouch, 1997; van de Wouw *et al.*, 2009). For the last six decades CWR have been increasingly used in crop breeding due to advances in species and taxonomic knowledge, genomics, breeding techniques and the reduction in cost and availability of biotechnological methods (Maxted and Kell, 2009; McCouch *et al.*, 2013). Numerous crops have been successfully improved by utilising CWR genes including: improved yield in potato (Gur and

Zamir, 2004); nutritional quality in cassava (Prescott-Allen and Prescott-Allen, 1988) and pest resistance in rice (JiUng *et al*., 2014).

In terms of economic worth, successful introduction of beneficial genes from CWR to major crops is currently valued at between 68 (PwC, 2013) and 115 billion US dollars annually (Pimental *et al*., 1997). However, as individual CWR have been known to contribute traits worth 250 million US dollars per annum to their related crop industry (Hunter and Heywood, 2011); these estimates may be understating the full contributing value of all CWR to agriculture.

Although CWR use is increasing, Maxted *et al.* (2012b) stress that breeders use of these resources varies significantly between crops and they are currently only being used systematically for a few major crops (barley *Hordeum vulgare* L., cassava *Manihot esculenta* Crantz, potato *Solanum tuberosum* L., rice *Oryza sativa* L., tomato *Solanum lycopersicum* L., and wheat *Triticum aestivum* L.). However for breeders to fully utilise the potential of CWR genetic resources, they must be readily available from seed genebanks and other germplasm repositories and, consequently, adequately conserved in the wild (Maxted *et al*., 2012b; McCouch *et al*., 2013). A point endorsed by key policy documents such as the International Treaty for Plant Genetic Resources for Food and Agriculture (FAO, 2001), the Global Strategy for Plant Conservation (CBD, 2010a), Aichi Biodiversity targets for 2020 (CBD, 2010b) and the United Nations Sustainable Development Goals for 2030 (United Nations, 2016), all of which promote the *in situ* and *ex situ* conservation and sustainable utilisation of CWR.

Despite their obvious value to human food security, CWR are, along with other biodiversity worldwide, threatened in their natural habitats with severe range reduction, and even extinction, and are currently under conserved (FAO, 2010). The threats to CWR populations and their genetic diversity are intensive farming and overgrazing, land use change, urbanisation, competition from invasive alien species and less directly climate change (Jarvis *et al*., 2008; Ford-Lloyd *et al*., 2011; Ureta *et al*., 2011; Kell *et al*., 2012). Castañeda-Álvarez *et al.* (2016) recently reviewed *ex situ* representation of CWR associated with 81 global priority crops in gene banks and out of 1076 CWR taxa found that 313 (29.1%) taxa have no *ex situ* conserved germplasm and a further 257 taxa are represented by fewer than ten accessions. The study concluded that 84.9% of global priority CWR were ranked as high or medium priority for further collecting and Dempewolf *et al.* (2013) report that systematic global *ex situ* collection has begun.

However, as Ford-Lloyd and Maxted (1993) noted, applying *ex situ* conservation techniques alone will not secure crop gene pools and provide the diversity required by users; a complementary approach is required that involves both the application of *in situ* and *ex situ* conservation techniques. Maxted *et al*. (2012b) highlighted the lack of progress with *in situ* CWR conservation, with only a handful of CWR genetic reserves reported globally, many of which do not meet the necessary quality standards proposed by Iriondo *et al*. (2012). As *in situ* CWR conservation approaches enable long term continued adaptation to changing environmental conditions, allowing novel genetic diversity to develop in response to climate change, there is a need to balance the *ex situ* initiative with parallel *in situ* action.

To help secure global food security, the urgent need for *in situ* CWR conservation has been stressed by several authors (Gadgil *et al.*, 1996; Maxted *et al.*, 1997a; Safriel *et al.*, 1997;

CBD, 2010a, b; FAO, 2010; FAO, 2011a) and, more precisely, the establishment of a network of CWR *in situ* reserves has been called for (Maxted and Kell, 2009; FAO, 2011c; ECPGR, 2012; FAO, 2014). The FAO (2013) held a Technical Workshop to explore the options and means for establishing a global network of reserves for *in situ* CWR conservation and raise awareness of the social and economic value of CWR, but concluded such a network requires further investigation, not least in the identification of the priority populations to be conserved *in situ*. Here we present a global *in situ* CWR gap analysis to identify these populations that together might constitute a global network of genetic reserves for priority CWR conservation, utilising, where possible, existing protected areas, maximising genetic diversity coverage and planning for longevity against climate change.

3.3 Methods

3.3.1 Determining target CWR and compiling occurrence data

Target CWR related to 167 crops vital to global food security and farmer income provision, were identified for analysis based upon close genetic relationships with these crops (gene pool 1B–2, or taxon group 1B–3) and known/potential use in crop breeding using the Harlan and de Wet CWR Inventory (Vincent *et al*., 2013) and GRIN Global CWR Portal (GRIN Global, 2015). CWR were recorded at the species level due to low numbers and unreliable taxonomy of occurrence records for sub taxa.

Occurrence records for all target CWR species were obtained from an online repository of CWR data (Castañeda-Álvarez *et al.,* 2016b) and then edited to remove: non-target taxa, cultivated occurrences, species occurrences outside of their native range, occurrences with no coordinates and inaccurate occurrences (coordinates with greater than 10km potential inaccuracy). Native species ranges were taken from the Germplasm Resources Information Network (GRIN) and the Harlan and de Wet Inventory (GRIN Global, 2015). CWR nomenclature in the occurrence record database was standardised to match GRIN's nomenclature.

3.3.2 Species distribution modelling

The MaxEnt algorithm was chosen to model the potential distributions of target CWR due to its strong performance against other modelling algorithms particularly when using small occurrence datasets, its requirement of presence only data and its wide use in biodiversity conservation studies (Elith *et al.*, 2006). Potential distributions were used rather than occurrence records only, as many species had low numbers of unique records and the occurrence records were considered not to be representative of the full distributional range of the CWR.

In order to produce potential distributions, MaxEnt requires environmental input variables and occurrence data to predict species ranges across a given landscape (Phillips *et al.,* 2006). A total of 27 variables (Supplementary Table 3.1) were classified into three subsets: edaphic, geophysical and climatic factors, for use in MaxEnt. The three sets of variables were subjected to stepwise variance inflation factor (VIF) analysis per CWR, using the 'USDM' package in R (Naimi, 2015) to remove collinear variables prior to MaxEnt modelling. Variables were represented by rasters at 2.5 arc minutes resolution (~5km at the equator).
To prevent overfitting and improve the species distribution models (SDMs) for *in situ* reserve planning, species variable layers were masked to the CWR native geographical area

(Anderson and Raza, 2010; Merow *et al.,* 2013). Ten thousand random background points were selected from each CWR native area to train MaxEnt models. MaxEnt was run using a five-fold cross validation technique to maximise small sets of occurrence records, using the reduced set of variables specific to each CWR. To assess the validity of models produced, the following criteria proposed by Ramírez-Villegas *et al.* (2010) were applied: (a) the five-fold average of the test Area Under the Test of the Receiver Operating Characteristic (ROC) curve (ATAUC) was greater than 0.7, (b) the standard deviation of the ATAUC for the five individual folds was lower than 0.15, and, (c) the proportion of the potential distribution where the standard deviation was greater than 0.15 was less than 10% of the total. Binary presence/absence maps were produced for accepted models by applying the maximum training sensitivity plus specificity (MAXTRSS) logistic threshold as this thresholding method has been found to consistently perform well compared to others (Liu *et al.,* 2013). Where MaxEnt produced models that did not meet the validation criteria, or had fewer than 10 unique occurrence records, CWR potential species distributions were approximated using a 50km buffer around each individual geo-referenced occurrence (Hijmans *et al.,* 2001).

Successful models were projected into the future using a no-migration scenario for all taxa to establish 'worst case' CWR conservation priorities and, in particular, identify promising *in situ* sites for climate change tolerance (D'Amen *et al.,* 2011). Thirty climate scenarios that informed the IPCC fifth report were obtained from the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) data portal with relative concentration pathway (RCP) 4.5 for the year 2070. The CWR MaxEnt models were projected into the 30 future climate scenarios and then averaged to produce a final future model, which was thresholded by the MAXTRSS to produce future binary presence/absence maps. The future maps were overlaid with the current potential distribution maps per species to identify areas that are most likely tolerant to climate change, and thus more suitable for long term *in situ* CWR conservation.

3.3.3 Genetic diversity assessment

To effectively conserve CWR *in situ* for future utilisation, the genetic diversity of individual populations must be taken into account at the planning stage, to ensure maximum coverage in protected areas and prevent genetic erosion in the wild. Due to the number of CWR occurrence records involved in the study that lacked quality genetic diversity data, environmental niche was used as a proxy to estimate and discriminate potential genetic diversity. The ecogeographic land characterisation (ELC) method (Parra-Quijano *et al.*, 2012a) was used to create a niche map of the native country range of each CWR by clustering the non-collinear variables from the edaphic, geophysical and climatic subsets, then combining the cluster values to produce a unique ELC category (referred to as adaptive scenario ─ ASc throughout) using the program CAPFITOGEN (Parra-Quijano *et al.*, 2014). ELC maps were then overlaid with current and future potential CWR distributions to determine the breadth of AScs and, by proxy, genetic diversity covered by each CWR.

3.3.4 *In situ* CWR gap analysis

The current state of *in situ* conservation for globally important CWR is unknown; therefore it is necessary to identify which CWR are not covered by the protected area network to ensure their long term conservation in the wild. To assess the state of current *in situ* CWR conservation globally, a gap analysis was undertaken to determine the overlap between CWR potential distributions with global protected areas. A comprehensive spatial dataset containing the geographical location of the worlds protected areas was retrieved from the Protected Planet portal (www.protectedplanet.net, downloaded 25/05/2016). Individual protected area polygons were dissolved to produce a global presence/absence layer of protected areas. Presence of potential distributions, with corresponding AScs, within protected areas was then identified for each species and each crop type. Results further indicate the percentage loss of protected area coverage and the percentage loss of AScs for each CWR in protected areas estimated for 2070 under a worst case no-dispersal scenario.

3.3.5 Prioritising areas for *in situ* conservation

Marxan is a widely used conservation planning program that employs simulated annealing to solve complex conservation problems whilst meeting user defined representation targets of biodiversity features for minimal cost. The scenario run in Marxan was to determine the most effective reserve network to conserve every target CWR/ASc combination in a minimum number of grid cells. Grid cells that contain protected areas were locked in to the final solution to maximise the use of the existing protection network and reduce the potential costs of acquiring land for new reserves outside of the network.

Marxan requires four compulsory input files in order to run: the planning unit file, the species file, the planning unit versus species representation file and the input parameters file. The planning unit file was created by listing the identification number of every terrestrial cell from a global grid with resolution five arc minutes (~ 10 km at the equator); planning unit cost was set to 10 if cells overlapped with the protected area network or 50 if there was no overlap. To create the planning unit versus species representation file, species distribution maps and their associated AScs were overlapped with the planning unit cells to determine which cells held which CWR/AScs. Where possible, the CWR distributions used in Marxan were those predicted to be climate change tolerant for 2070, to ensure that sites chosen would be more likely to provide longer term CWR protection; for CWR where future climate models predicted full loss of current range or there was no valid MaxEnt model, the current potential distribution was used in Marxan. The species file was created by listing every CWR/ASc combination and assigning them a unique identifier number. Marxan targets were set to achieve at least one of every CWR/ASc combination in the final network. The species penalty factor (SPF), which allows prioritisation of biodiversity elements for selection within Marxan, was calibrated using the method described by Ardron *et al.* (2010). The final SPF was set to one for all species as they were deemed of equal importance and to ensure equal chance of selection. An additional file was included, the boundary file, which listed the location of each planning unit cell in regard to its neighbours. This file was added to improve the spatial clumping of selected sites, as it is often easier and cheaper to conserve closely located sites rather than dispersed ones. In the input parameters file, the Marxan scenario was set to carry out 100 runs of 100,000,000, iterations. The boundary length modifier (BLM), which helps to produce spatially clumped networks of potential conservation sites, was calibrated using the technique described by Ardron *et al.* (2010) and set to 0.001. The potential sites from the resulting Marxan solution were then ranked by fewest number of planning units followed by cheapest cost; the top ranked solution was chosen as the most suitable overall solution.

Reserves in the top ranked Marxan solution were prioritised for conservation action using complementarity ranking (Rebelo, 1994) to maximise taxonomic and genetic diversity in the network. The algorithm first selects the site with highest species richness count, then chooses the second site that will be most complementary to the first, i.e. the site which will increase the net number of species most significantly for the total solution. This process continues until all species are represented in the final solution or a user defined maximum number of sites is selected. This algorithm was written and executed in Python on the sites selected by the final Marxan solution. Two implementation scenarios were run through the Rebelo ranking algorithm. The first, an 'optimal' scenario in which it is assumed reserves can be set up anywhere globally without constraint, and the second, a 'practical' scenario where the algorithm is first run on only sites containing protected areas, to maximise existing protection, then run again in a complementary fashion, on sites containing no protected areas and that do not contain the species already identified for conservation in the first run. All CWR were given equal importance/weighting in the algorithm and it was run until all CWR/ASc combinations were represented in the final solution at least once. The top 150 priority sites within the ideal Marxan network were then mapped for the optimal scenario and the practical scenario sites.

3.4 Results

A total of 1425 species related to 167 crops were identified as priority CWR for improving food security and farmer income provision, however 164 of these species had no good quality occurrence records, leaving a total of 1261 possible CWR species to analyse. Of the 1261 remaining species, 791 were modelled using MaxEnt; 67 of those species models failed the validation criteria, and their current distributions were estimated using 50km circular buffers around occurrence points, along with the remaining 470 CWR species.

Current CWR distributions were predicted to occur across the majority of the temperate, tropical and subtropical regions, excluding polar and extreme arid areas (Figure 3.1). However, the spread of priority CWR worldwide is heterogeneous and is concentrated in specific geographical areas. The most CWR species rich area was the Mediterranean basin where 105 species were modelled in a single 100 km^2 grid cell. Other areas of significant species richness included southern Europe, the Caucasus, the Fertile Crescent, Indochina, Eastern USA, the western coast of USA, the Andes and central eastern South America. Regions of high CWR species richness were also highly coincident with well-known key areas of biodiversity richness including Centres of Plant Diversity (UNEP-WCMC, 2013) and Myers' Biodiversity Hotspots (Myers, 1988; Mittermeier *et al*., 2011), particularly in Indochina, western coastal USA, the Andes and the Mediterranean.

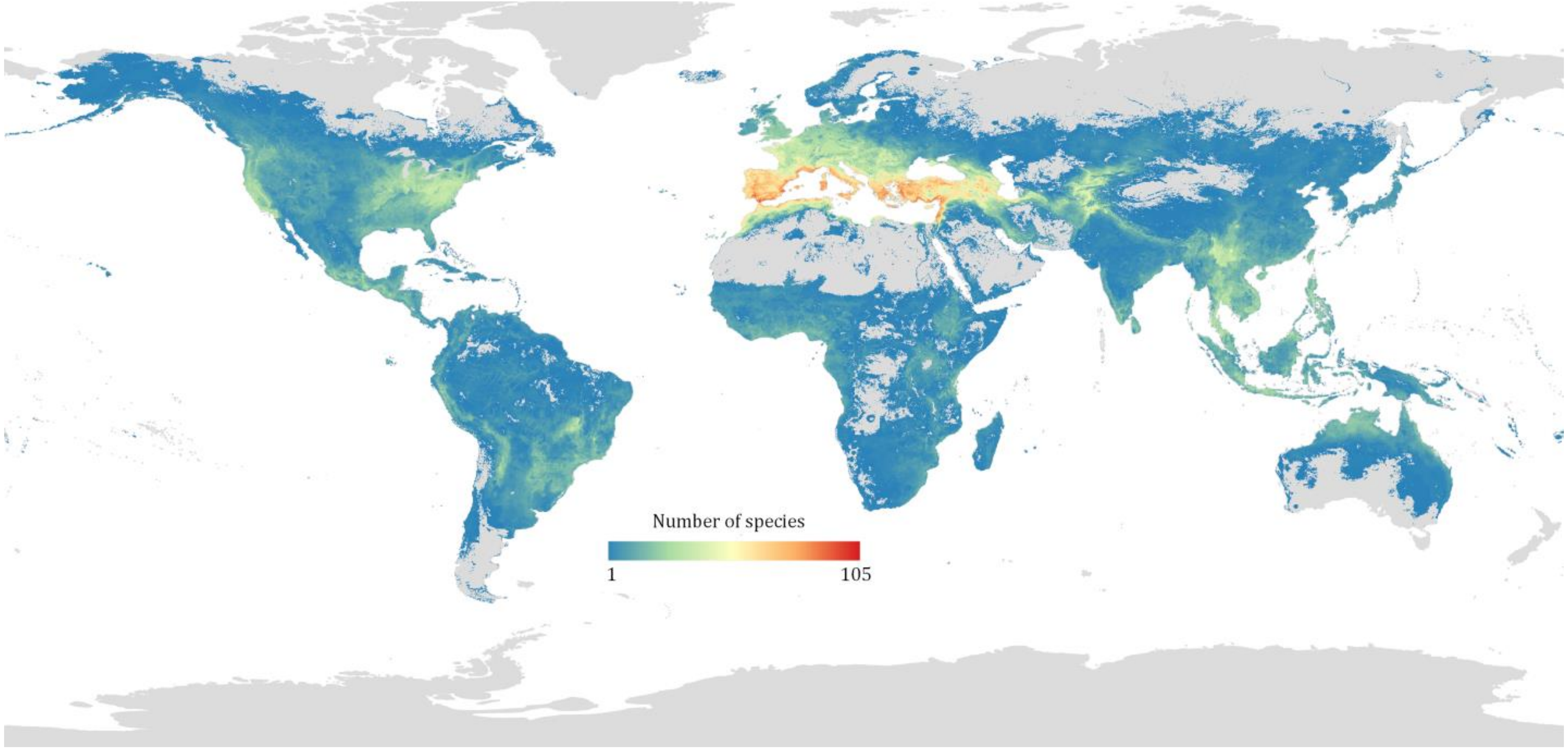

Figure 3.1 CWR species richness map for the current climate at five arc minutes resolution

Table 3.1 shows the gap analysis results for each individual CWR consolidated under shared crop types. Some CWR belong to more than one crop type, for example, *Brassica cretica* Lam. belongs to gene pool 2 of both kale and oil seed rape, so belongs in both the leafy or stem vegetables category and oilseed crops category. The numbers of crops and CWR belonging to each crop type varied greatly with the fewest crops being sugar crops and other crops with two — sugar beet and sugar cane, and cotton and woad respectively — and the most being leguminous crops with 30. Numbers of CWR per crop type ranged from 15 for citrus fruits to 264 for root, bulb, or tuberous vegetables, which contains crops with large gene pools such as potato and cassava. All crop types have at least one CWR with no occurrence records; however some crop types are better represented than others. Cereals and leguminous crops have the fewest number of CWR with no occurrences with less than 5% of their total number, conversely, citrus fruits have the highest proportion of CWR with no occurrences with 46.67%. To gain an insight into how well the crop types are represented in the dataset the number of CWR with no occurrences and the number of CWR with less than 10 unique occurrence records were combined to find the proportion of under-represented CWR. The crop type with poorest representation across its gene pool was citrus fruits with 93.33% of its CWR having less than 10 unique occurrences, followed by beverages (68.11%), other crops (63.89%), tropical and subtropical fruits (53.49%) and spice crops (51.61%).

To improve reserve planning for long term *in situ* conservation, CWR with valid MaxEnt distribution models were projected into the year 2070 using future climate variables. The number of CWR projected to lose 50% or more of their current ranges were totalled under the appropriate crop type; the root, bulb, or tuberous vegetables have the most CWR facing significant distribution loss with 20 CWR, followed by cereals with 19 and leguminous crops with 17 CWR (Table 3.1). No modelled CWR from grape crops or citrus fruits were found to lose greater than 50% current distribution. In terms of proportion of MaxEnt modelled CWR that are set to lose greater than 50% of their current potential distribution, spice crops is the most vulnerable with 26.67% of all modelled CWR losing significant distribution in 2070, followed by sugar crops (14.29%), cereals (13.67%) and beverages (13.64%). Under the consolidated crop types, CWR are well covered by the existing protected area network with grape CWR having the least coverage at 14.66% and CWR of leafy or stem vegetables having the most protected area coverage at 32.84% on average (Table 3.1). However, the results for loss of predicted area coverage for 2070 show that the majority of crops will be impacted by climate change under a no migration scenario, losing roughly one fifth of current protected area coverage on average per CWR. The crops least effected appear to be citrus fruits with only 4.57% loss with the most effected being sugar crops with 31.37%.

Table 3.1Consolidated gap analysis results for different crop types. PA = Protected Area

Crop type	**No. crops**	**No. CWR**	**CWR with no occurrences**	**CWR with 1><10 occurrences**	**CWR with >50% distribution loss in 2070**	**Average current PA cover for CWR (%)**	**Average loss of PA cover for CWR in 2070 (%)**
Berries	4	55	5	12	1	30.54	15.70
Beverage crops	5	69	26	21	3	25.56	24.98
Cereals	16	157	5	13	19	21.63	25.39
Citrus fruits	7	15	7	7	0	18.79	4.57
Fruit-	10	42	3	11	2	17.60	23.23

bearing vegetables							
Grapes	3	20	2	5	0	14.66	20.33
Leafy or stem vegetables	15	89	11	29	4	32.84	23.89
Legume crops	30	208	10	52	17	22.67	21.89
Nuts	8	73	8	29	3	24.06	19.98
Oilseed crops	11	81	7	11	4	22.50	19.47
Pome fruits and stone fruits	10	128	19	42	3	24.27	21.97
Root, bulb, or tuberous vegetables	20	264	24	77	20	21.74	22.13
Spice crops	14	31	8	8	4	27.27	24.16
Sugar crops	2	20	1	5	2	30.27	31.37
Tropical and subtropical fruits	10	172	34	58	7	19.27	23.35
Other crops (e.g. fibres)	2	36	2	21	1	22.78	28.89

As part of the gap analysis, the current conservation status of CWR genetic diversity within the existing protected area network was recorded for each species then summarised under related crop types. Figure 3.2 highlights the averaged proportion of CWR genetic diversity covered by the existing protected area network and the predicted losses of genetic diversity within these areas under the projected climatic changes in 2070. All crop types have at least 70% of averaged CWR genetic diversity within the existing protected area network, with the highest being 91.85% for berries and the lowest, 70.68% for other crops. In terms of predicted loss of genetic diversity in protected areas, berries and spice crops are expected to experience the least loss with only 6.53% reduction of genetic diversity, whilst other crops are expected to lose 31.16% of genetic diversity within protected areas, followed by fruit bearing vegetables at 19.76% and leguminous crops at 19.49%.

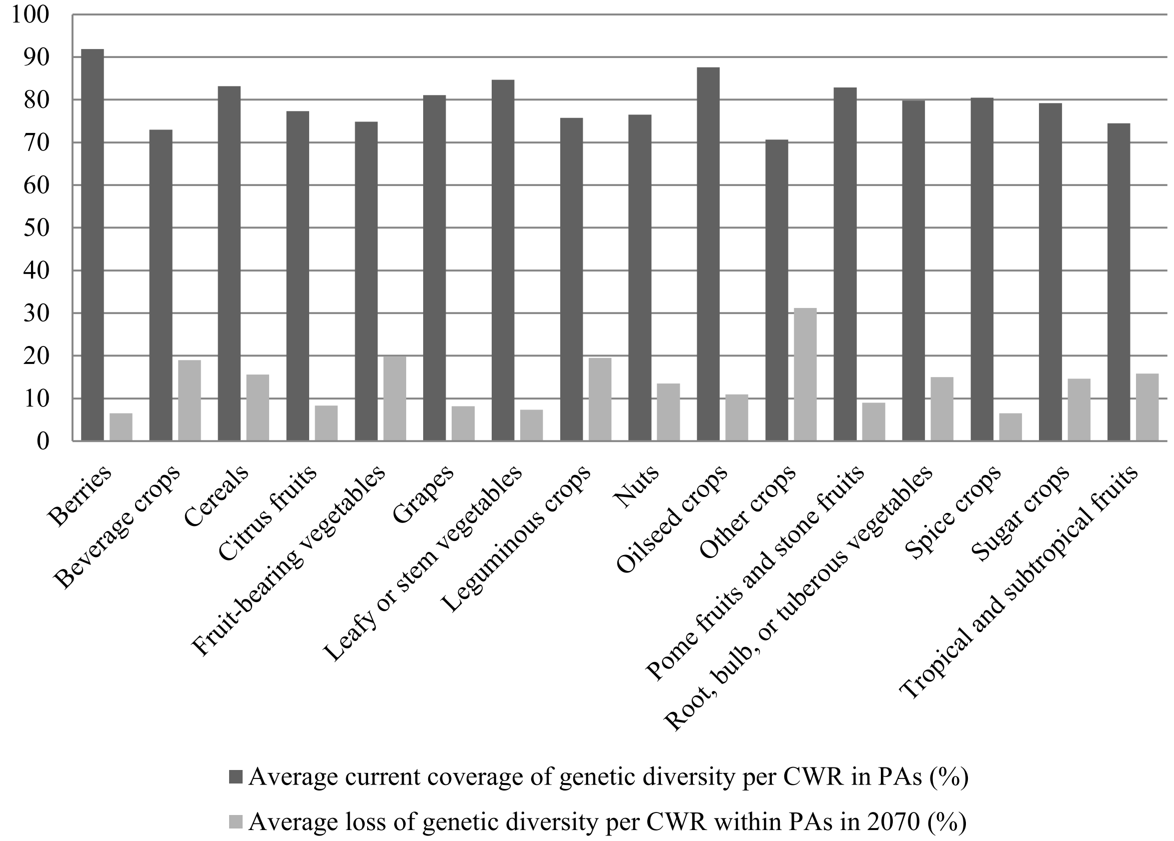

Figure 3.2 Current and projected loss of genetic diversity in protected areas (PAs) for CWR grouped by crop type

Individual CWR in general were found to be well represented in the current protected area network; only 35 (2.5%) of the studied species from 28 crops were distributed exclusively outside of protected areas (Supplementary Table 3.2). These included seven CWR from gene pool 1B such as wild *Pennisetum glaucum* (L.) R.Br. related to pearl millet; *Prunus argentea* (Lam.) Rehder, related to almond and *Prunus sibirica* L., related to apricot. The top five CWR found to have the highest proportion of distribution in protected areas were: *Coffea costatifructa* Bridson, *Ficus glareosa* Elmer, *Manihot alutacea* D.J.Rogers & Appan , *Beta patula* Aiton and *Beta nana* Boiss. & Heldr. If we consider a threshold of 50% or more of CWR genetic diversity within protected areas to be well conserved, then 112 of the assessed CWR are under conserved and 91% of CWR are well covered by the existing protected area network.

In terms of future model projections only two species, *Vicia hyaenicyamus* Mouterde and *Zea perennis* (Hitchc.) Reeves & Mangelsd., are predicted to go extinct under a no migration scenario by 2070. However, a further 83 species are predicted to lose greater than 50% of their current range by 2070. These include *Arachis batizocoi* Krapov. & W. C. Greg., *Arachis appressipila* Krapov. & W. C. Greg., *Manihot gabrielensis* Allem, *Vigna keraudrenii* Du Puy & Labat and *Oryza nivara* S. D. Sharma & Shastry, which all expect to lose over 80% of their current potential distribution. In regard to CWR genetic diversity in 2070, 15 CWR are projected to lose over 50% of their current genetic diversity by 2070 through distribution loss, in addition to this 39 individual CWR are expected to lose over 50% of genetic diversity that is currently passively conserved in the protected area network. Further details on the *in situ* gap analysis results for individual CWR can be viewed in Supplementary Table 3.2.

To explore the options for implementing CWR *in situ* conservation globally, two site prioritisation scenarios were applied to the sites chosen by Marxan; the ‘optimal’ scenario and the ‘practical’ scenario. Figure 3.3 shows the top ranked 150 sites prioritised for CWR genetic conservation under the optimal scenario, which cover 899 CWR (71.29% of all assessed CWR) and 4592 CWR/ASc combinations (31.94% of combined CWR genetic diversity) from 160 crops. Only 17 of the top 150 sites contained protected areas. The crops not covered in the top 150 sites consist of: amur grape, brazil nut and cardamom, horseradish, mandarin, pimento and yautia. The top 10 sites in this scenario are located in: (1) southern Spain, (2) northeastern Turkey, (3) northern Israel, (4) northern Spain , (5) eastern Turkey, (6) southern China, (7) western USA, (8) Brazil, (9) southern Turkey, and, (10) northern Borneo, Malaysia. These sites contain 321 CWR (25.46% of assessable CWR) and 964 CWR/AScs (6.71% of total genetic diversity) from 98 crops.

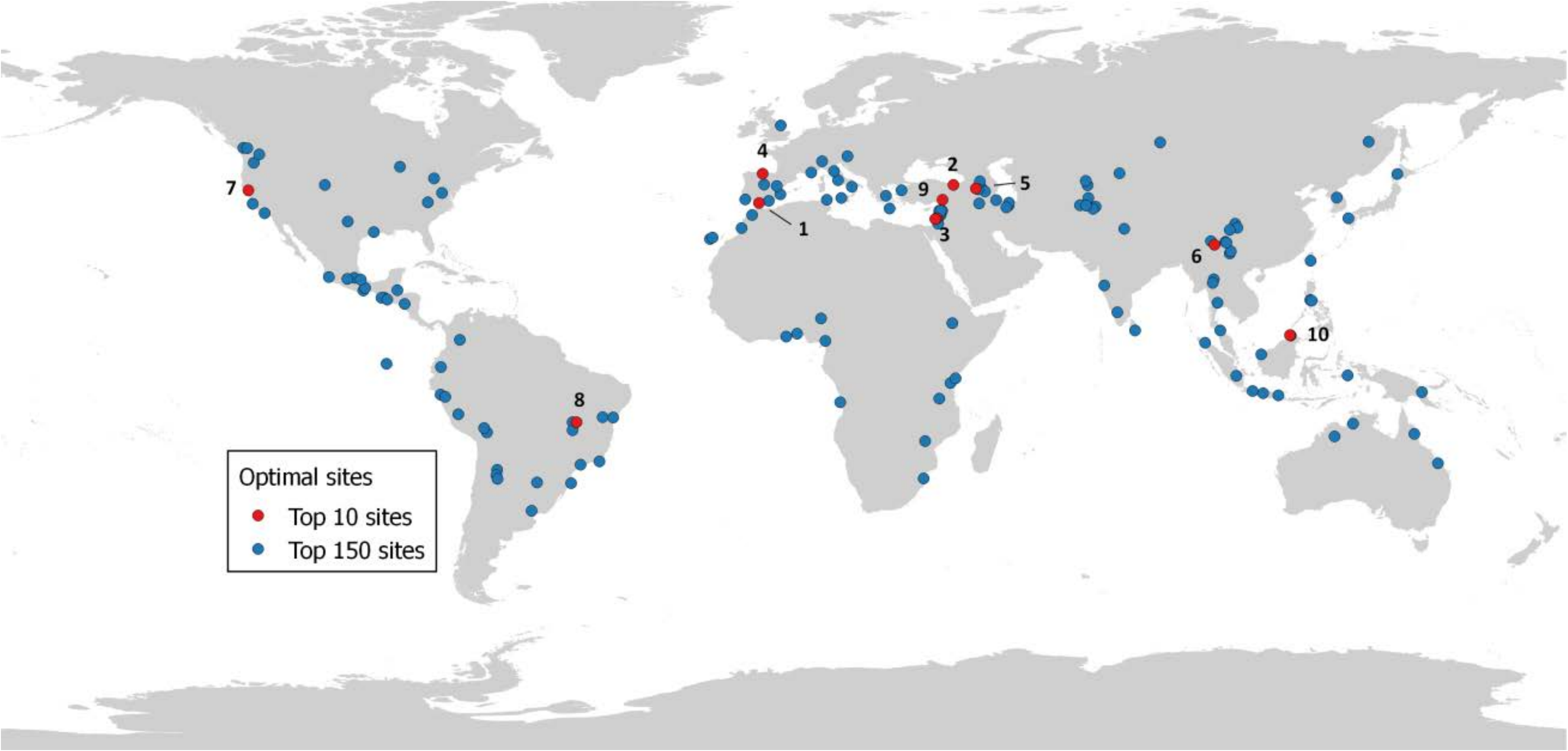

Figure 3.3 Top 150 sites for global *in situ* CWR conservation under the 'optimal' scenario

To maximise the use of the existing protected area network and reduce the likely costs of setting up new CWR reserves, sites selected by Marxan were prioritised using the ‘practical’ scenario. Figure 3.4 shows the top 100 ranked sites within protected areas and the top 50 sites outside of the existing protected area network under the practical scenario, which covers 829 CWR (65.74% of assessed CWR), with 416 (32.99%) in protected areas, and 4008 CWR/AScs (27.88% of total genetic diversity), with 3758 (26.14%) in protected areas, from 157 crops in total. The crops not covered in these top 150 sites are: horseradish, grapefruit, sweet lime, mandarin, cardamom, amur grape, pimenta, yautia, brazil nut and aji.

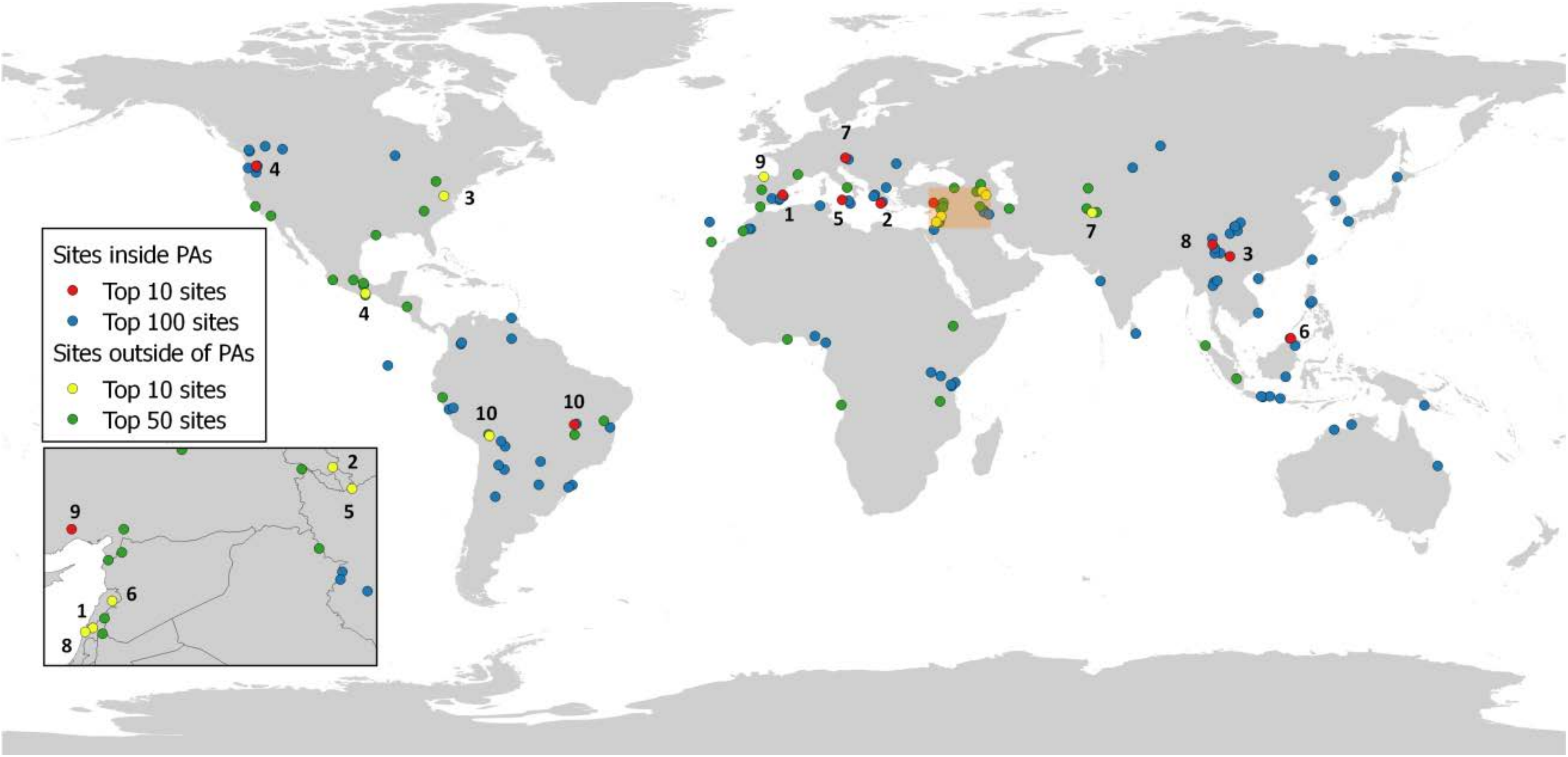

Figure 3.4 Top 150 sites for global *in situ* CWR conservation under the 'practical' scenario, with magnification on the Fertile Crescent and Caucasus to show the priority site locations therein

The top ten sites for CWR *in situ* conservation for both inside and outside the protected area network are described in detail in Table 3.2 and Table 3.3, respectively to highlight areas where *in situ* CWR conservation could begin. The top 10 sites listed in Table 3.2 contain a combined total of 270 unique CWR (21.41% of assessed CWR) and 726 CWR/AScs (5.05% of all genetic diversity) all contained within protected areas. 50% of the top 10 sites are found in the Mediterranean basin and mainland Europe; additionally, two sites are located in East Asia, one in Southeast Asia, one site in North America and one site in South America. The protected areas that overlap the top 10 sites in Table 3.2 cover a range of designations including: Special Protection Areas (Birds Directive) – Spain; Scenic areas (IUCN VI – China; Provincial/Regional Nature Reserves (IUCN V) – Italy; Sites of Community Importance (Habitats Directive) – Greece; World Heritage sites – China; and, Indigenous Areas – Brazil.

Table 3.2 Details of the top 10 sites inside of protected areas in the practical implementation scenario

Site No.	**Country**	**Location**	**No. CWR**	**No. unique CWR added to 'practical' reserve network**	**No. unique CWR/ASc combinations added to 'practical' reserve network**	**Protected Areas**
1	Spain	Simat de la Valldigna, Benifairó de la Valldigna, Alzira, Tavernes de la Valldigna,	85	85	155	Montduver-Marjal de la Safor (Special Protection Area (Birds Directive), Regional); Serres del Montduver i Marxuquera (Site of Community

		Xeraco, Barx, Xeresa and Gandia, Valencia province				Importance (Habitats Directive), Regional); Parpallo-Borrell (Nature Place (Local Interest), National); Serra de Corbera (Site of Community Importance (Habitats Directive), Regional)
2	Greece	Messinia and Laconia districts in the Peloponnese	58	15	91	Oros Taygetos (Site of Community Importance (Habitats Directive), Regional); Lagkada Trypis (Special Protection Area (Birds Directive), Regional)
3	China	Border of Xishan, Chenggong and Kunming counties in Kunming district	42	42	78	Dianchi (Scenic area, National, IUCN VI)
4	USA	Intersection of Skamania, Oregon and Hood River and Klickitat counties in Washington	32	30	68	Wygant (State Natural Area, National, IUCN V)
5	Italy	Monreale, Corleone, Godrano, Piana Degli Albanesi and Marineo in Palermo province Sicily	71	10	61	Riserva naturale orientata Bosco della Ficuzza, Rocca Busambra, Bosco del Cappelliere e Gorgo del Drago (Regional/Provincial Nature Reserve, National, IUCN IV);

						Rocca Busambra e Rocche di Rao (Site of Community Importance (Habitats Directive), Regional)
6	Malaysia	Northern Ranau district, Sabah	37	33	61	Kinabalu (National Park and ASEAN Heritage Park, National, IUCN II)
7	Austria	North central Liezen district	30	6	59	Warscheneck-Gruppe (Landscape Protection Area, National, IUCN V); Ennstal von Ardning bis Pruggern (Landscape Protection Area, National, IUCN V); Ennstal zwischen Liezen und Niederstuttern (Special Protection Area (Birds Directive), Regional); Putterer See (Nature Reserve, National, IUCN IV); Schluchtwald der Gulling (Site of Community Importance (Habitats Directive), Regional)
8	China, Myanmar	Gongshan Derung and Nu county, China and Khawbude township, Myanmar	37	10	57	Three Parallel Rivers of Yunnan Protected Areas (World Heritage Site, International)
9	Turkey	Çamliyayla district, Mersin province	59	15	50	Cehennem Deresi Milli Parkı (National); Kadıncık Vadisi Milli Parkı (National)
10	Brazil	Intersection of Minaçu and	24	24	46	Ava-Canoeiro (Indigenous Area,

	Colinas do Sul districts, Goias		National)

The top 10 sites listed in Table 3.3 complement the 100 sites in protected areas chosen in the practical scenario, and contain a combined total of 283 unique CWR (22.44% of total assessed CWR) and unique 836 CWR/AScs (5.82% of total genetic diversity) from 106 crops, however, they only add 205 (16.26% of assessed CWR) species and 531 CWR/AScs (3.69% of total genetic diversity) from 89 crops to the existing 100 sites in protected areas. 50% of the sites in Table 3.3 were located in the Fertile Crescent and Caucasus region; additionally, two were found in Central and North America, one in South America, one in Spain and one in Afghanistan.

Table 3.3 Details of the top 10 sites outside of protected areas in the practical implementation scenario

Site No.	**Country**	**Location**	**No. CWR**	**No. unique CWR added to 'practical' reserve network**	**No. unique CWR/ASc combinations added to 'practical' reserve network**
1	Israel	North central HaZafon province	81	44	86
2	Armenia	Eastern Vayots Dzor province	57	30	75
3	USA	Warren, Page and Rappahannock counties, Virginia	30	23	58
4	Mexico	Dist. Yautepec and Dist. Miahuatlan, Oaxaca	31	26	51
5	Armenia,	South west Zangilan	73	20	50

	Azerbaijan	province, Azerbaijan and south east Syunik province, Armenia			
6	Lebanon	Central Baalbek, Beqaa province	56	9	47
7	Afghanistan	Central eastern Dara-i-Pech, Kunar province	46	17	42
8	Israel	Northern Haifa district	79	3	42
9	Spain	Camaleño, Cillorigo de Liébana, Potes, Peñarrubia and Tresviso, Cantabria province	74	14	41
10	Bolivia	Yanacachi, Coripata and Coroico municipalities in La Paz	26	19	39

To conserve the combined top 10 sites in the practical scenario for CWR conservation inside and outside existing protected areas would only require 8.72×10^{-4} % of world's total terrestrial area and cover 475 individual CWR (37.67% of assessed CWR) and unique CWR/ASc combinations. Similarly, to conserve the top 150 sites presented in the 'optimal' or 'practical' scenario would require only 0.01% of the world's total terrestrial area.

3.5 Discussion

In the past, conservation actions worldwide have mostly focussed on the protection of threatened or rare taxa and ecosystems, whilst some species of great utility to humanity have been overlooked and undervalued. However, the combined threats of climate change and massive global population expansion have highlighted the need for adaptation and improvement in current agricultural systems, and that conserving and utilising CWR for breeding climate change tolerant varieties is of paramount importance. Activity on *in situ* conservation of CWR has been neglected, with the *in situ* conservation needs of CWR related to the world's most important crops for food security having never been analysed systematically. Furthermore, the few sites that are dedicated to CWR conservation worldwide, such as those in: Nicaragua (Ramsar, 2016); Izmir, Turkey (Tan and Tan, 2002); Ammiad, Israel (Anikster *et al*., 1997); and, Erebuni, Armenia (Gabrielian and Zohary, 2004) are unlikely to meet the genetic reserve quality standards for CWR *in situ* conservation proposed by Iriondo *et al.* (2012). To improve knowledge on the gaps in current CWR *in situ* conservation actions, this paper provides a detailed, systematic, *in situ* gap analysis of current and projected priority CWR species distributions and genetic diversity and recommends areas for the establishment of complementary CWR genetic reserves worldwide.

The occurrence dataset used in this analysis highlights that many CWR are poorly represented in genebanks, herbaria and occurrence databases worldwide, with 164 CWR having no occurrence records and a further 470 CWR having fewer than 10 occurrences, supporting the recommendations of Castañeda-Álvarez *et al.* (2016) that greater targeted *ex situ* CWR collection efforts are needed. This would enable greater accuracy within *in situ* CWR conservation planning efforts, increase representativeness in genebanks and allow breeders access to a wider variety of genetic resources. Some crop gene pools are particularly under represented, such as citrus fruits, tea and tropical and sub-tropical fruit bearing trees, possibly due to unresolved taxonomy in the case of *Citrus* or difficulty in collecting and storing recalcitrant seeds in the case of tropical fruit trees. Results show that CWR of well-studied crops like cereals and legumes are well represented as expected, as more breeding work has been focussed on these crops. This imbalance in CWR representativeness needs to be addressed now, before CWR populations suffer greater genetic erosion and loss, and for breeders to utilise this great resource and provide more resilient crops. The major CWR *ex situ* collecting work organised by Dempewolf *et al.* (2013) will undoubtedly help to address this.

The gap analysis results reveal a surprisingly high number of CWR distributions are present in the existing protected area network. However, the existing protected area network does not contain every CWR; 35 CWR are found solely outside protected areas and should be targeted for CWR conservation. However, the high representativeness of CWR in protected areas could be affected by overfitting of SDMs. Differences in sampling intensity and sampling methods may lead to a biased set of species occurrence records which could affect the reliability of the modelled distribution. Furthermore SDMs do not take into account biotic interactions, and for future climate models, other effects on distribution such as phenotypic plasticity or evolutionary adaptation are not explored (Pearson and Dawson, 2003). Conversely, CWR with few total occurrence records cause a greater percentage change if found in or outside of protected areas, due to the greater weight each occurrence record holds in total. These issues can be resolved by obtaining more occurrence data which is representative of the species range.

Genetic diversity data per CWR in the analysis was estimated using environmental niche as a proxy. Further study and experiments are required to test whether this approach is truly appropriate for such a wide range of species. However in the near future, incorporating actual genetic diversity and characterisation data for individual occurrences into conservation planning will be possible due to the rapidly reducing costs of biotech methods and via mass sequencing and characterisation projects such as DIVSEEK (http://www.divseek.org/) which aims to sequence CWR germplasm held in genebanks.

The gap analysis results reveal that the predicted effects of climate change on potential distributions are different for each individual CWR even within crop gene pools; therefore, it is vital conservation strategies are adapted to individual species requirements. CWR such as *Zea perennis* and *Vicia hyaeniscyamus*, which are predicted to go extinct under a no migration scenario, and *Arachis appressipila*, *Vigna keraudrenii* and *Manihot gabrielensis* which are predicted to lose over 50% of existing range by 2070, should be prioritised for *in situ* conservation. A new reserve is required particularly for *Vicia hyaeniscyamus*, which does not have any distribution within the current protected area network and is predicted to go extinct under a no migration scenario. Further work is required to analyse the level of fragmentation CWR distributions are likely to face in the future as this would affect *in situ* conservation requirements and increase the need to plan for corridors between established reserves to ensure populations do not become isolated, enable migration and to maintain gene flow between populations.

The sites identified within this study represent the first formation of a global network of CWR reserves. The ideal or ‘optimal’ scenario covers 899 CWR and 4592 CWR/ASc combinations from 160 crops in the top ranked 150 grid cells. However, only 17 of these grid cells contain protected areas. This scenario is not realistic to implement due to the low number of potential sites inside the existing protected area network and the costs and difficulty in procuring land for new reserves. The ‘practical’ scenario which covers 829 CWR (416 in protected areas) and 4008 CWR/AScs (3758 in protected areas) from 157 crops in the top 150 sites is the preferred conservation implementation choice due to the greater utilisation of existing protected areas, reduction in potential costs of obtaining new land for protected areas and quicker establishment of CWR reserves, thus conservation of CWR, due to the protection already in place. However, ‘ground truthing’ is required to ensure that the CWR do exist in these sites identified for *in situ* conservation. The managers of the protected areas coincident with sites selected in the ‘practical’ scenario should be contacted and asked if the target CWR are present, or, if this is not possible, national agencies responsible for CWR protection could survey the potential sites and report back on CWR existence.

The establishment of the top 150 sites in the practical scenario would vastly increase the proportion of CWR and their genetic diversity conserved globally for only a fraction of the world’s total terrestrial area, and contribute substantially to satisfying Aichi Targets 11 and 17 (CBD, 2010b), Activity 4 of the FAO’s second global plan of action (GPA) (FAO, 2011a) and UN sustainable development goal (SDG) 2 (UN, 2016). However, due to the fact that natural CWR distributions do not follow political boundaries, two priority sites within the ‘practical’ scenario have been selected on country borders –China/Myanmar and Armenia/Azerbaijan – these sites will be impractical to establish in their current location. The initial foundation of CWR reserves identified under the ‘practical’ scenario can be built upon by including more realism into the conservation planning problem, such as threat layers, locking out regions where CWR conservation may be impractical currently – such as Syria, Crimea and along political borders –and weighting of species by gene pool level or IUCN Red List assessment to ensure those species get priority during selection.

Normally, *in situ* conservation methods focus on establishing and expanding protected areas to achieve species protection. However, as protected areas are becoming progressively like isolated islands of biodiversity (DeFries *et al.,* 2005), experiencing increasing degazettement, downgrading and downsizing (Mascia and Pailler, 2011), are increasingly threatened by destructive industrial activities and habitat disruption (Laurance *et al*., 2012; WWF, 2016) and are generally poorly managed and underfunded (Leverington *et al*., 2010), other methods of conservation need to be explored to ensure long term security. On this note, different CWR also require different conservation strategies. Some CWR such as legumes and grasses are ruderal and prefer disturbed habitats, such as roadside verges; these habitats are not usually found in protected areas which often seek to preserve pristine environments. CWR with this behaviour may be more suited to less formal conservation, outside of protected areas. This could take the form of community conservation areas, such as the Parque de la Papa in Peru where local people conserve wild potato species, or even local stakeholders monitoring road verges for ruderal species. Other types of CWR species, such as tropical fruit bearing trees, will require more formalised *in situ* conservation and require the presence of a protected area, due to population structure, difference in lifecycle and habitat preference. Therefore it is necessary to assess the conservation needs of each individual CWR and create appropriate strategies accordingly.

To improve the long term management, monitoring, and knowledge of *in situ* CWR conservation worldwide, a new online database should be created recording any information on *in situ* CWR action including: which taxa are being conserved; the location of the conservation taking place; coordinate or vector data showing the location of conservation; population size and genetic diversity data; who is responsible for maintaining and monitoring the site; and, the overlap with protected areas if applicable. As it is can be very difficult to get information on definite species within protected area and access management plans, this database updated by the CWR community would be extremely helpful for informing future *in situ* conservation planning.

CHAPTER 4

A comparison of crop wild relative hotspots with biologically and ecologically important geographical regions; a case study with Myers' biodiversity hotspots

This chapter is being prepared for publication as:

Vincent, H., Hole, D. and Maxted, N. (2016) A comparison of crop wild relative hotspots with biologically and ecologically important geographical regions; a case study with Myers' biodiversity hotspots (in prep.)

Author contributions:

Conceived and designed the study: **HV**, NM

Data collation and preparation: **HV**

Performed analysis: **HV**

Analysed results: **HV**

Wrote the paper: **HV**

Critically reviewed the paper: **HV**

4.1 Abstract

Biodiversity is currently experiencing exceptional loss due to the activities of humans, negatively impacting the eco-system services on which humanity relies. Additionally, human induced climate change is likely to severely impact agriculture worldwide, leading to reduced yields for some crops and regions. Crop wild relatives (CWR), the wild cousins of domesticated crops, contain a wide breadth of genetic diversity not found in cultivated crops, which could be used for breeding new climate tolerant varieties. However, CWR are under-conserved in the wild, thus jeopardising this resource.

Funds for CWR conservation activities are often limited; to conserve efficiently, strategies can prioritise *in situ* actions to areas of existing biodiversity conservation or protection. This analysis examines whether CWR protection could benefit from conservation in areas of high biodiversity, in particular Myers' Biodiversity Hotspots. Global CWR hotspots were defined from statistically significantly spatially clustered areas of high CWR richness. Biodiversity hotspots as a whole had significant overlap with CWR hotspots with the highest coincidence in the Mediterranean basin (91.28%) and the California Floristic Province (90.96%). Overall, the Mediterranean basin, Irano-Anatolian, Caucasus and Tropical Andes hotspots showed greatest promise for *in situ* conservation of CWR.

4.2 Introduction

The rate of species extinction is currently higher than ever known, outpacing previous mass extinctions with a rate of loss 100 times greater than would be expected, compared to estimated background levels (Ceballos *et al.*, 2015). In fact, by 2050 we could lose up to 37%

of known species worldwide (Thomas *et al*., 2004). This large scale loss of species, and the genetic diversity within them, is most often attributed to anthropogenic actions including destruction of habitats and changes in land use, which are at an unprecedented high (Butchart *et al*., 2010). This in turn is wreaking havoc on the ecosystem services on which humans rely (Cardinale *et al.*, 2012) and is contributing to the negative effects of climate change (IPCC, 2014). To reduce the rate of species extinction more efficient conservation strategies must be employed by prioritising complementary areas which, with protection and monitoring, can maximise the genetic, species and ecosystem biodiversity that is conserved (Mittermeier *et al*., 2011).

One of the ecosystem services on which humans are totally reliant is food production. Climate change and an increasing human population are having a huge, negative impact on food production, increasing the demand for improved crop varieties that are able to cope with changing conditions. Indeed, the IPCC (2014) estimates that some major agricultural crops may lose up to 25% of their yield post 2050 due to changes in climate if crop variety adaptation is not implemented.

Crop wild relatives (CWR), the wild and weedy cousins of domesticated crops, are a crucial key to overcoming these challenges due to their wide genetic diversity and tolerance of marginal environments; features which can be used to breed new climate resilient and higher yielding crop varieties (Ford-Lloyd *et al.*, 2011, 2014). CWR have been used to improve nutritional qualities, yields and pest and disease resistance of crops via plant breeding for over 70 years (Maxted and Kell, 2009). Past successes of the introduction of CWR traits into crops have included: the introgression of leaf rust and powdery mildew resistance from *Hordeum* *bulbosum* L. into barley (Pickering *et al.* 1998), conference of drought tolerance from *Oryza rufipogon* Griff. to rice (Zhang *et al.*, 2006) and improved protein content transferred from *Aegilops ovata* L. to wheat (Sharma and Gill, 1983).

Despite their importance, CWR and their conservation in the wild has been neglected, both *in situ* (Maxted *et al.*, 2008a, 2015) and *ex situ* (Castañeda Álvarez *et al.*, 2016), leaving taxa vulnerable to genetic erosion and extinction in their natural habitats (Maxted and Kell, 2009; Ford-Lloyd *et al.*, 2011). Until recently, the identity of the priority CWR for the World's most important crops was unknown, making systematic conservation action impossible at a global level. However, to address this, the Harlan and de Wet Global CWR Inventory (Vincent *et al.*, 2013) was created and has been a major resource in several national CWR conservation strategies (Fielder *et al.*, 2015; Phillips *et al.*, 2014), a global CWR *ex situ* collection strategy (Castañeda Álvarez *et al.*, 2016) and in guiding CWR *ex situ* germplasm collections (Dempewolf *et al.*, 2013). To complement the global *ex situ* strategy devised by Castañeda Álvarez *et al.* (2016), Vincent *et al.* (Chapter 3 of this thesis) examined the current state of global *in situ* CWR conservation based upon a major collection of CWR occurrence data from herbarium and genebank records of wild populations. This occurrence data was used to carry out reserve planning techniques to suggest new sites for conservation which enhance the existing protected area network and plan for changes in species future distributions which may occur due to climate change. Maintaining populations of CWR *in situ* is vital for the ongoing evolution of useful traits including resistance to pests and disease, tolerance of marginal and degraded habitats and resilience to climate change, for use in crop breeding. However, the window of opportunity for *in situ* CWR conservation won't remain open forever, so it is vital to find smart and cooperative approaches to accomplish protection of these important species in the wild before this resource is lost. Current biodiversity conservation funding globally is considered to be insufficient and the shortfall is likely to impede accomplishing the CBD targets for 2020 (McCarthy *et al.,* 2012; Waldron *et al*., 2013); therefore any new sites for CWR protection would benefit from coincidence of other threatened biodiversity and promotion/inclusion of CWR within existing biodiversity conservation actions to concentrate resources where they are likely to have the biggest effect.

One scheme into which the integration of CWR conservation could be achieved is the Biodiversity Hotspots concept developed by Myers in 1988, as many CWR are known to be native to highly biodiverse areas of the world. The Biodiversity Hotspots concept was developed as a way of prioritising regions that contain outstanding plant species endemism and have experienced significant loss of natural habitat, to efficiently utilise limited conservation funds and help prevent species extinction in highly threatened areas (Myers, 1988; Myers *et al.*, 2000). Initially Myers (1988) described 10 hotspots based upon presence of many endemic plant species and substantial loss of habitat, including Western Ecuador, Peninsular Malaysia and Colombian Choco. These were then increased to 18 with the addition of areas such as southwestern Sri Lanka, the Western Ghats in India and Tanzania (Myers, 1990). Further refinements in the hotspot delimitation process have led to a total of 35 hotspots (Figure 4.1) currently recognised for high levels of plant endemism and substantial levels of habitat loss (Mittermeier *et al.*, 1998, 2004, 2011; Myers, 2003)

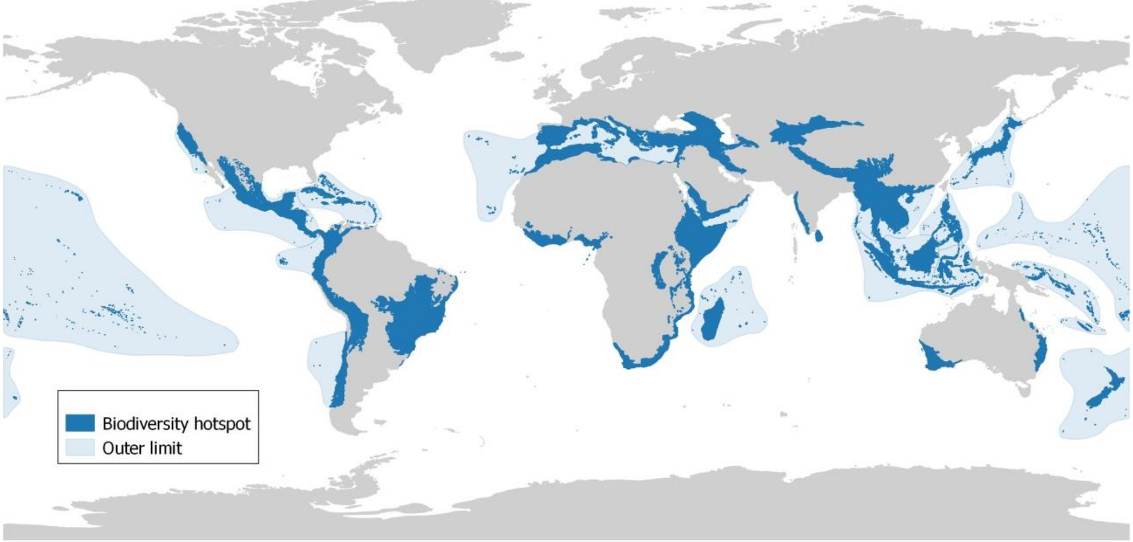

Figure 4.1 The 35 Myers' Biodiversity Hotspots (CEPF, 2011; Mittermeier *et al.,* 2011)

Myers' Biodiversity Hotspots have received considerable economic investment since their inception (Dalton, 2000) with an estimated one billion US dollars spent on conservation within these areas up to 2011 (Mittermeier *et al.*, 2011). The regions continue to receive steady investment for conservation programmes from organisations such as Conservation International, which uses the Biodiversity Hotspots as its core area of action and invested over 100 million US dollars in conservation programmes in 2015 (Conservation International, 2016), and the Critical Ecosystem Partnership Fund (CEPF) which since the year 2000 has invested 191 million US dollars into conservation projects in 24 of 36 Biodiversity Hotspots (CEPF, 2015). Steady funding and a strong scientific and public profile make Biodiversity Hotspots strong candidates for long-term *in situ* conservation of CWR.

In this paper we investigate the suitability of Biodiversity Hotspots for CWR conservation by defining important CWR hotspots globally and investigating the coincidence and degree of overlap between current CWR distributions, CWR hotspots and Biodiversity Hotspots. We also examine locations in to which *in situ* CWR conservation could be incorporated and ways in which this could be implemented to enhance existing conservation actions, maximise the impact of conservation funds and increase the profile of CWR worldwide.

4.3 Methods

4.3.1 Target CWR and data collation

Target crops and their associated CWR were identified for inclusion in the analysis based upon their importance for global food security and farmer income provision. CWR related to 167 key crops were prioritised for analysis based upon their known/potential use in crop breeding and the level of genetic relationship with associated crops (gene pool 1B–2, or taxon group 1B–3) using the GRIN Global CWR Portal (GRIN Global, 2015) and Harlan and de Wet CWR Inventory (Vincent *et al.*, 2013).

Occurrence data for target CWR was downloaded from a comprehensive CWR occurrence online database (Castañeda-Álvarez *et al.,* 2016) and edited to remove: cultivated taxa and occurrences, non-target taxa, occurrences with no coordinate data, poorly georeferenced occurrences (those with greater than 10 km potential inaccuracy) and CWR occurrences outside of their native distribution. Species nomenclature in the occurrence dataset was standardised to follow GRIN's taxonomy. CWR native ranges were obtained from the Harlan and de Wet Inventory and GRIN (GRIN Global, 2015). To overcome difficulties with inaccuracies in taxonomy of occurrence records at the sub taxa level and the low numbers of occurrence records at the sub taxa level, CWR were named at the species level.

4.3.2 Species distribution modelling

To maximise the occurrence records of each species, species distribution modelling was used to produce potential distribution maps. The MaxEnt method, which uses the maximum entropy principle to make predictions on potential distributions utilising presence only occurrence data and environmental variables, was chosen to model species distributions due to its extensive application in ecological and biodiversity conservation studies.

Twenty seven environmental variables were chosen as inputs for MaxEnt, and classified into edaphic, bioclimatic or geophysical categories. To improve the accuracy of MaxEnt distribution predictions, collinear variables were removed from the total set of factors by stepwise variance inflation factor (VIF) analysis (Merow *et al.,* 2013) using the 'USDM' package in R (Naimi, 2015).

MaxEnt models were trained using ten thousand background points taken from the native range of each species and run under a five-fold cross validation technique using the non-collinear variables identified for each species. The fitness of each predictive model was evaluated using three methods, which all had to be satisfied to qualify the model as valid. The methods were: (a) the five-fold average of the test Area Under the Test of the Receiver Operating Characteristic (ROC) curve (ATAUC) must be greater than 0.7, (b) the standard deviation of the ATAUC for each fold must be lower than 0.15, and, (c) the proportion of the potential distribution where the standard deviation was greater than 0.15 must be less than 10% of the total (Ramírez-Villegas *et al.*, 2010). Presence/absence maps showing potential species distribution were created for each valid model by applying the maximum training sensitivity plus specificity logistic threshold (Liu *et al.*, 2013). For CWR where predictive models failed the validation test, or had fewer than 10 unique occurrence records, potential distributions were estimated using a circular 50 km buffer around each occurrence point (Hijmans *et al.*, 2001). All variables utilised and distribution models created had a spatial resolution of 2.5 arc minutes (~5 km at the equator).

4.3.3 Discrimination of CWR hotspots

To assess the potential of Myers' Biodiversity Hotspots as a conduit for CWR *in situ* conservation, CWR geographical hotspots needed to be identified. A CWR species richness map at the 5 arc minutes (~10 km at the equator) resolution was produced by overlaying the potential CWR distributions, created using MaxEnt and the 50 km circular method, and counting the number of unique CWR per grid cell. The gridded CWR richness map was used as input in the Hotspot Analysis tool in ArcGis 10.2 to find geographical areas that were deemed significant high CWR richness hotspots. The Getis-Ord Gi* statistic (Figure 4.2) underpins the Hotspot Analysis tool and is calculated for every input feature. The statistic assumes a null hypothesis of Complete Spatial Randomness (CSR) for the features being assessed, meaning that the grid cells with high CWR richness counts are hypothetically assumed to be randomly spatially distributed about the study area. The observed sum of the grid cell values combined with its neighbours is then calculated and compared to the expected sum of these values under the assumed null hypothesis. If the observed sum of values differs greatly from the expected sum of values then a significant Z score is produced, meaning that the observed sum greatly varies from the mean under a normal distribution. The Z scores are produced in this manner for every cell in the study area and given a corresponding p value to define the confidence with which the null hypothesis can be rejected for that cell. For example a cell with a Z score of >2.58 has a corresponding p value of 0.01, therefore with a confidence level of 99% it can be assumed that the results are not the product of a random distribution and the null hypothesis can be rejected. For each cell in the CWR richness grid, neighbours were set as those sharing a boundary edge or corner. Grid cells that had a positive Z score with significance level of 1% or less ($p < 0.01$), indicating substantial clustering, were selected as being spatially significant CWR rich hotspots.

The Getis-Ord local statistic is given as:

$$G_i^* = \frac{\sum_{j=1}^{n} \omega_{i,j}\omega_j - \bar{X}\sum_{j=1}^{n} \omega_{i,j}}{S\sqrt{\frac{\left[n\sum_{j=1}^{n} \omega_{i,j}^2 - \left(\sum_{j=1}^{n} \omega_{i,j}\right)^2\right]}{n-1}}}$$

where ω_j is the attribute value for feature j, $\omega_{i,j}$ is the spatial weight between feature i and j, n is equal to the total number of features and:

$$\bar{X} = \frac{\sum_{j=1}^{n} x_j}{n}$$

$$S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - (\bar{X})^2}$$

The G_i^* statistic is a z-score so no further calculations are required.

Figure 4.2 Formula diagram of the Getis-Ord Gi* statistic. Extracted from ArcGIS (2015).

4.3.4 Comparing CWR hotspots and potential CWR *in situ* sites with Biodiversity Hotspots

In order to identify specific areas for CWR *in situ* conservation inside Myers' Biodiversity Hotspots, spatial vector data for the 35 regions was obtained from the CEPF website (CEPF, 2011). To enable comparison between Biodiversity Hotspots and global CWR hotspots, each individual Biodiversity Hotspot was rasterised to a grid with 5 arc minutes resolution, to enable manipulation in R. One hundred and fifty potential reserve sites derived from a 'practical' conservation scenario which attempts to maximise CWR coverage in existing protected areas for the *in situ* conservation of CWR were obtained from Vincent *et al.* (Chapter 3 this thesis) and overlaid with the CWR hotspots and Biodiversity Hotspots to assess congruence. Finally, Biodiversity Hotspots were prioritised for *in situ* CWR conservation action by ranking the hotspots by most to least percentage overlap with CWR hotspots, highest to lowest number of CWR species in each Biodiversity Hotspot and highest to lowest number of potential reserve sites within Biodiversity Hotspots. The three rankings per Biodiversity Hotspot were then averaged and the highest ranking 10 Biodiversity Hotspots were selected as priorities for *in situ* CWR conservation action.

4.4 Results

The final occurrence dataset contained 334,527 records for 1425 target CWR identified as priority species due to their close genetic relationship and utility in breeding for 167 crops vital to food security and farmer income provision. The target CWR were comprised of 183 gene pool (GP) 1B species, 596 GP2 species, 30 taxon group (TG) 1B species, 154 TG2 species, 113 TG3 species, 53 provisional gene pool (PGP) 1B species, 79 PGP2 species, 103 species confirmed as being used in breeding and 67 species with potential use for crop breeding. Good quality occurrence records were totally unavailable for 164 of the species, leaving a total of 1261 CWR that could be modelled. A further 470 species were poorly represented in terms of unique occurrence records, with fewer than 10 per CWR and were modelled using the 50 km circular buffer approach. The remaining 791 CWR species distributions were modelled using MaxEnt.

CWR hotspots were defined using the Getis-Ord Gi* statistic in ArcMap 10.2. Figure 4.3 shows that CWR hotspots are spread throughout the temperate, sub-tropical and tropical areas of the world. Hotspots of significant species richness are particularly concentrated around the Mediterranean basin and Europe, spreading to the Fertile Crescent, the Caucasus and finally Central Asia (including northern India). In North America, a large cluster of CWR hotspots is located on the eastern coast of the USA spreading inland towards Kansas, and another is located on the west coast of the USA spreading from California to Washington. In Central America the CWR hotspots start from central Mexico and continue down to northern Nicaragua. In South America patches of CWR hotpots appear along the Andes, beginning in western Peru and heading through Bolivia, down to northern Argentina. Further clusters in the same region are found in eastern Paraguay and the border around Paraguay and Argentina. In Brazil the major CWR hotspots are centred in Goiás, São Paulo and Minas Gerais, with smaller clusters of hotspots spreading south from these states to Rio Grande do Sul. In mainland Africa small fragmented hotspots can be found in the west, along the coastal side of Côte d'Ivoire, Nigeria and Cameroon. Similar small hotspots can be found in southwest Ethiopia and around the coastal borders of Tanzania and Kenya. Further CWR hotspots are found in southern India and Sri Lanka, northern Australia, southern China, Indonesia, Malaysia, the Philippines, Myanmar, Thailand, Laos and Cambodia. The global CWR hotspots constitute only 7.44% of the world’s terrestrial area and cover 1019 target CWR species from 160 key crops. Crops (and their CWR) not contained within the CWR hotspots consist of: horseradish, brazil nut, aji, mandarins, cardamom, amur grape and yautia.

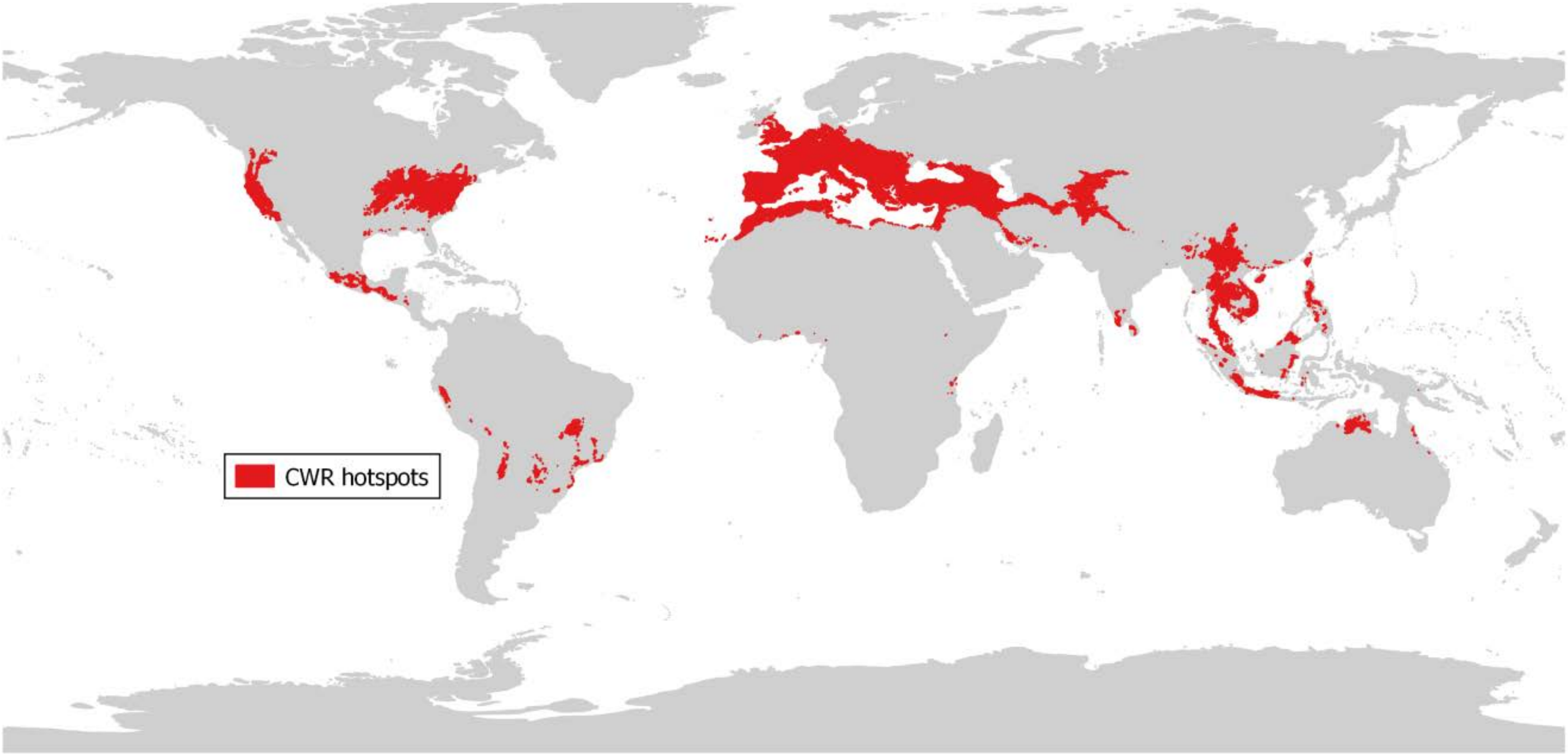

Figure 4.3 Global CWR hotspots at 5 arc minutes resolution

In terms of overlap between CWR hotspots and Biodiversity Hotspots, 25.94% of the total area of the Biodiversity Hotspots overlapped with the CWR hotspots, whereas over half (52.18%) of the terrestrial area covered by CWR hotspots was coincident with Biodiversity Hotspots. As a whole, Biodiversity Hotspots contain 1114 CWR (88.34% of total modelled CWR) potential distributions from 163 crops; the crops not covered were horseradish, cardamom, and amur and muscadine grape.

Table 4.1 further details the overlap, if any, between the individual Biodiversity Hotspots and CWR distributions, CWR hotspots and the 150 priority CWR *in situ* sites for conservation identified by Vincent *et al.* (Chapter 3 this thesis), in an effort to determine which Biodiversity Hotspots are most suited to CWR conservation. In total, 12 of the 35 Biodiversity hotspots worldwide have partial overlap with the CWR hotspots. Furthermore, four of the Biodiversity Hotspots have greater than 50% of their total area covered by the CWR hotspots; the Mediterranean basin with 91.28%, California Floristic Province with 90.96%, the Irano-Anatolian hotspot with 77.65% and the Caucasus hotspot with 75.76% coverage. In regard to the Biodiversity Hotspots with no overlap with CWR hotspots, two are located in the American continent, five in the African continent, five in the Australian continent and one in the Asian continent. The Biodiversity hotspots with the greatest number of unique CWR distributions within were the Mediterranean basin with 298 (23.63% of all modelled CWR), followed by the Irano-Anatolian hotspot with 206 (16.34% of all modelled CWR) and the Caucasus with 171 (13.56% of all modelled CWR). The Biodiversity Hotspots which overlapped with the fewest CWR distributions were New Zealand with no CWR, New Caledonia with three and Southwest Australia with six CWR. The Biodiversity Hotspots in total contained 81 of the 150 priority *in situ* sites for CWR conservation identified by Vincent *et al.* (Chapter 3 this thesis), however, 14 of the Biodiversity Hotspots contained no *in situ* sites at all. The Mediterranean basin hotspot covered the highest number of priority sites with a total of 30 (20% of the 150 priority sites) and also had the most top ranked sites with seven. Six additional Biodiversity Hotspots contained top ranked sites for *in situ* conservation; the Caucasus contained 2 top sites and the Mountains of South-west China, Mesoamerica, Cerrado, Tropical Andes and Sundaland hotspots all contain one top ranked site. The only Biodiversity Hotspot with no overlap at all with CWR distributions, CWR hotspots or priority *in situ* CWR sites was New Zealand.

Table 4.1 Details of Myers' Biodiversity hotspots overlap with CWR hotspots, individual CWR distributions and priority sites for *in situ* CWR conservation

Hot-spot ID	**Myers' hotspot**	**Proportion overlap with CWR hotspot**	**No. priority *in situ* conservation sites within Myers' hotspot**	**No. species within Myers' hotspot**	**No. related crops within Myers' hotspot**	**No. CWR in CWR and Myers' hotspot overlap**	**No. related crops in CWR and Myers' hotspot overlap**
H1	California Floristic Province	90.96	2	53	25	49	22
H2	Madrean Pine-Oak Woodlands	18.97	2	127	40	77	30
H3	Mesoamerica	13.51	3 (1 top 20 site)	112	35	90	34
H4	Caribbean Islands	0	0	19	15	0	0
H5	Tumbes-Choco-Magdalena	1.63	1	79	29	38	19
H6	Tropical Andes	6.25	12 (1 top 20 site)	163	37	108	26
H7	Cerrado	7.13	3 (1 top 20 site)	104	22	76	18
H8	Atlantic Forest	8.89	4	94	19	75	18
H9	Chilean Winter Rainfall and Valdivian Forests	0	0	12	9	0	0

H10	Mediterranean Basin	91.28	30 (7 top 20 sites)	298	79	296	78
H11	Irano-Anatolian	77.65	6	206	75	206	75
H12	Caucasus	75.76	4 (2 top 20 sites)	171	73	171	73
H13	Horn of Africa	0	0	60	41	0	0
H14	Eastern Afromontane	0.47	2	77	40	38	31
H15	Coastal Forests of Eastern Africa	2.79	1	44	25	31	22
H16	Madagascar and the Indian Ocean Islands	0	0	17	17	0	0
H17	Maputaland-Pondoland-Albany	0	0	29	23	0	0
H18	Cape Floristic Region	0	0	12	11	0	0
H19	Succulent Karoo	0	0	12	10	0	0
H20	Guinean Forests of West Africa	1.53	1	42	26	35	22
H21	Western Ghats and Sri Lanka	19.07	1	56	32	52	32
H22	Mountains of Central Asia	35.00	2	96	53	94	53
H23	Himalaya	12.51	1	148	79	139	79

H24	Mountains of Southwest China	28.19	5 (1 top 20 site)	95	54	88	49
H25	Indo-Burma	43.18	7	146	55	139	53
H26	Sundaland	25.08	10 (1 top 20 site)	103	35	99	34
H27	Philippines	28.15	2	49	29	47	28
H28	Wallacea	1.46	0	43	22	34	21
H29	Southwest Australia	0	0	6	4	0	0
H30	Forests of East Australia	1.90	0	28	14	24	14
H31	East Melanesian Islands	0	0	25	19	0	0
H32	New Caledonia	0	0	3	4	0	0
H33	New Zealand	0	0	0	0	0	0
H34	Japan	0	2	44	37	0	0
H35	Polynesia-Micronesia	0	0	14	10	0	0

There are nine Biodiversity Hotspots in the American continent as shown in Figure 4.4. The Biodiversity Hotspots in this region contain 27 priority sites for *in situ* CWR conservation including three top ranked sites, with one in a protected area. The California Floristic Province hotspot (H1) has the most CWR hotspot coverage in this region with 90.96% and two hotspots – the Chilean Winter Rainfall and Valdivian Forests and the Caribbean Islands - have no overlap with the CWR hotspots. One large cluster of CWR hotspots which is not covered at all by the Biodiversity Hotspots, but contains three priority sites for *in situ* CWR conservation is located on the eastern half of the USA. The key protected area for *in situ* CWR conservation in this region is the Ava-Canoeiro (Indigenous Area, National) in Goiás, Brazil.

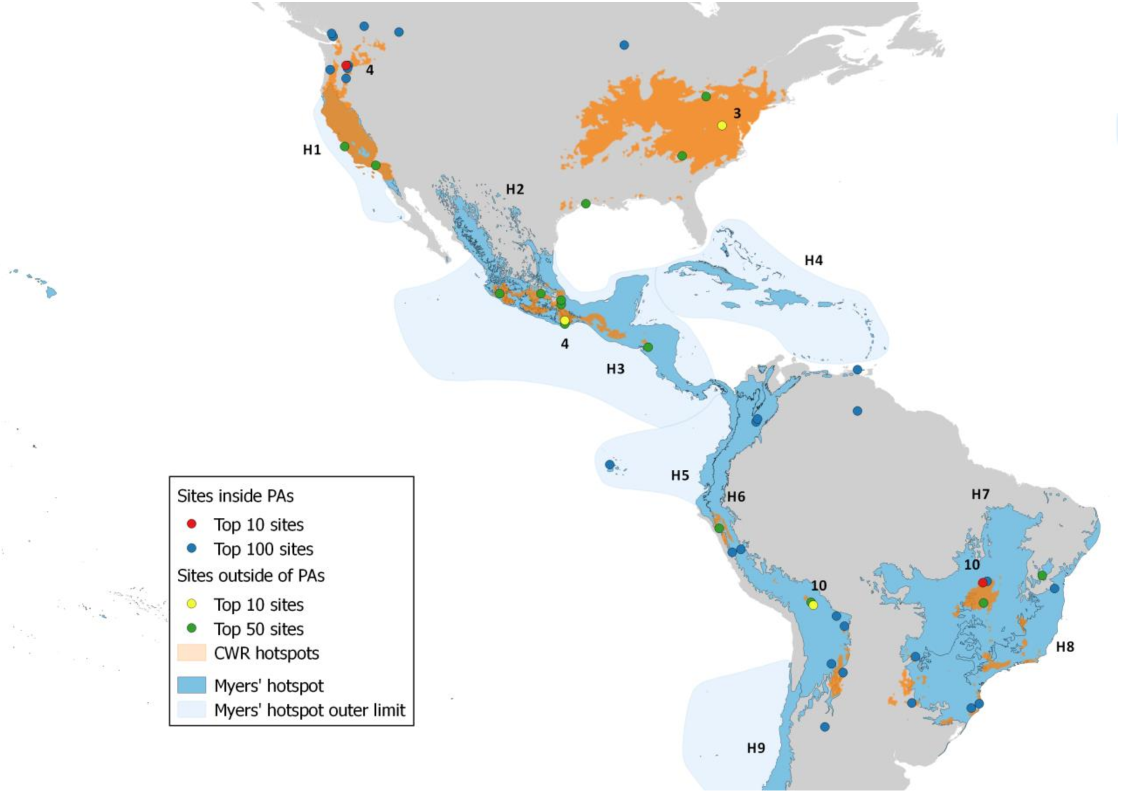

Figure 4.4 Myers' Biodiversity Hotspots, CWR hotspots and priority CWR *in situ* conservation sites in the American continent

In the Europe, Western Asia and African region there are a total of 11 Biodiversity Hotspots (Figure 4.5; Succulent Karoo, Cape Floristic Region and Maputaland-Pondoland-Albany hotspots are omitted). Biodiversity Hotspots in this region contain 44 priority sites for *in situ* conservation of CWR including nine top ranked sites, with four inside the existing protected area network. The Mediterranean basin hotspot has the most CWR hotspot coverage in this region with 91.28%; the Irano-Anatolian and Caucasus hotspots are similarly well covered with 77.65% and 75.76% respectively. Conversely, five of the Biodiversity Hotspots have no overlap with CWR hotspots; they are the Horn of Africa, Madagascar and the Indian Ocean Islands, Succulent Karoo, Cape Floristic Province and Maputaland-Pondoland-Albany. A large cluster of CWR hotspots covering the majority of European countries are not found in any Biodiversity Hotspot but contain two top ranked sites for *in situ* CWR conservation and a further two top 150 priority sites. The key existing protected areas for implementing *in situ* CWR conservation in this region are: Oros Taygetos (Site of Community Importance , Habitats Directive, Regional) – Greece; Riserva naturale orientata Bosco della Ficuzza, Rocca Busambra, Bosco del Cappelliere e Gorgo del Drago (Regional/Provincial Nature Reserve, National, IUCN IV), Rocca Busambra e Rocche di Rao (Site of Community Importance ,Habitats Directive,, Regional) – Italy; Aladağlar National Park (National) – Turkey; Serres del Montduver i Marxuquera (Site of Community Importance, Habitats Directive, Regional), Parpallo-Borrell (Nature Place, Local Interest, National), Serra de Corbera (Site of Community Importance, Habitats Directive, Regional) – Spain.

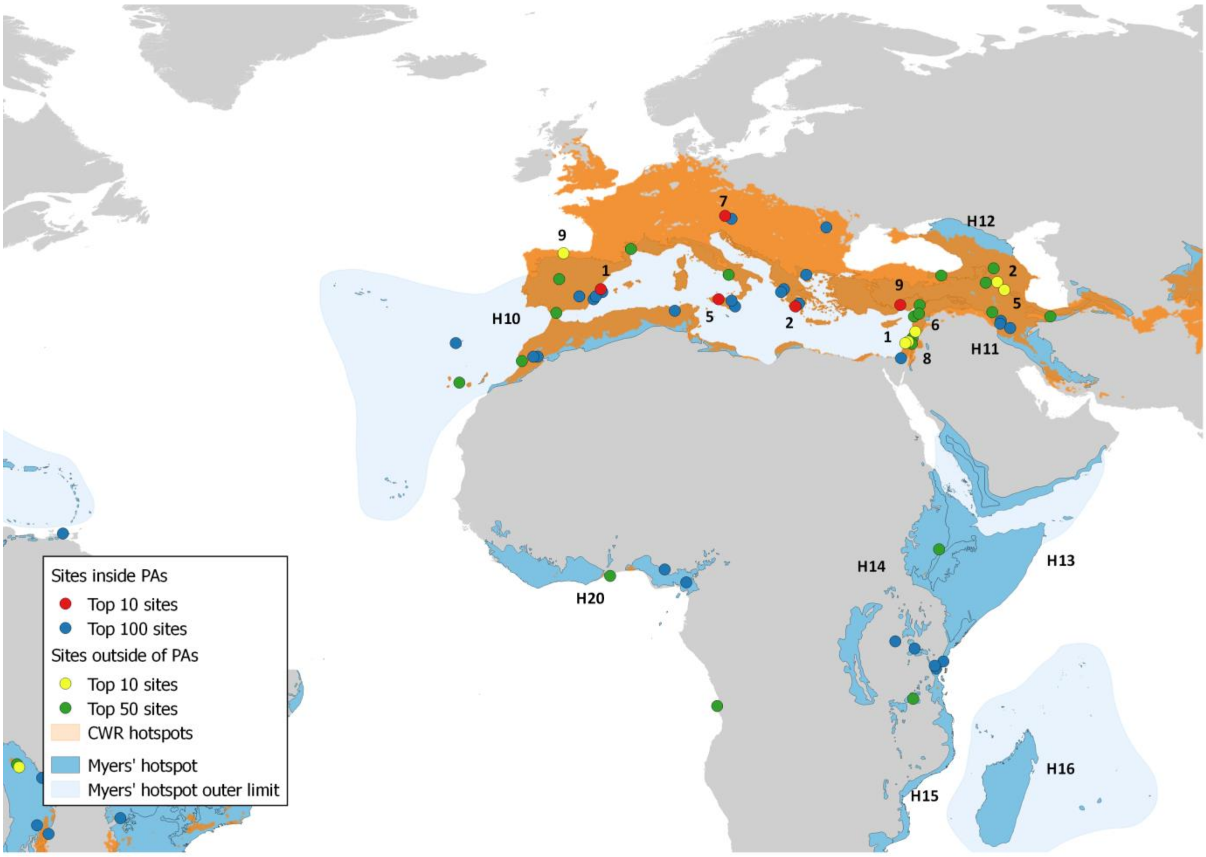

Figure 4.5 Myers' Biodiversity Hotspots, CWR hotspots and priority CWR *in situ* conservation sites in Europe, Western Asia and Africa

There are 15 Biodiversity Hotspots in the Central Asia, East Asia and Australasia region (Figure 4.6). The Biodiversity Hotspots in this region contain 30 priority sites for *in situ* CWR conservation, including two of highest priority within protected areas. The Indo-Burmese hotspot (H25) has the largest area overlap with CWR hotspots out of all Biodiversity Hotspots in this region with 43.18%, conversely, several Biodiversity Hotspots have no overlap at all including Japan, East Melanesian Islands and New Zealand. Key protected areas in this region which overlap the top ranked priority *in situ* sites for conservation are: the Three Parallel Rivers of Yunnan Protected Areas (World Heritage Site, International)– China/Myanmar and Kinabalu (National Park and ASEAN Heritage Park, National, IUCN II) – Malaysia.

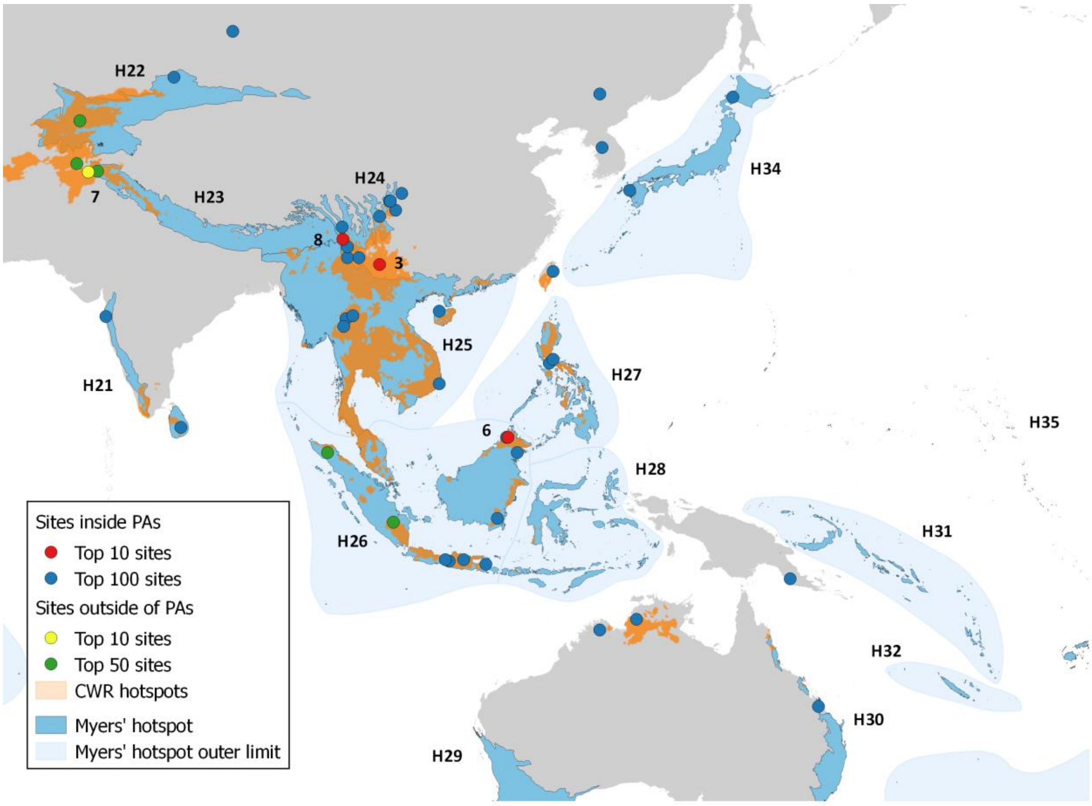

Figure 4.6 Myers' Biodiversity Hotspots, CWR hotspots and priority CWR *in situ* conservation sites in Central Asia, East Asia and Australasia

Biodiversity Hotspots were ranked for *in situ* CWR conservation action based upon the number of potential reserve sites within the hotspots, the percentage overlap with CWR hotspots and the number of CWR species in each Biodiversity Hotspot. The top 10 Biodiversity Hotspots prioritised for their potential contribution to CWR *in situ* conservation were the Mediterranean Basin, Irano-Anatolian, Caucasus, Tropical Andes, Himalaya, Indo-Burma, Madrean Pine-Oak Woodlands, Mesoamerica, Cerrado and Sundaland.

4.5 Discussion

CWR are a vital source of genetic diversity for breeding new crop varieties which are more efficient in terms of land, fertilisers and water inputs, able to cope with an unpredictable climate and the changes that brings in the environment, and feed an ever expanding population (Henry, 2014; Redden, 2015). However, CWR are poorly conserved, particularly *in situ* (Maxted *et al*., 2015), and are increasingly threatened in their natural habitats. To improve their conservation *in situ*, Vincent *et al*. (Chapter 3 this thesis) suggested 150 priority sites worldwide where *in situ* strategies could be implemented, whilst maximising CWR and genetic diversity coverage. This would aid in a reduction in biodiversity loss in terms of CWR species and genetic diversity, and help to achieve global targets for biodiversity conservation, and sustainable use (CBD, 2010a, 2010b; FAO, 2011b; United Nations, 2016) and ensure the long term protection of an important resource for adapting agriculture to climate change. However, resources for conservation, particularly economic resources, are often lacking therefore it is necessary to prioritise biodiversity and regions for protection to ensure maximal conservation returns for minimal economic spend. Working together with other biodiversity conservation agencies is one option to maximise CWR conservation (Mace *et al.,* 2000).

Although the concept of Myers' Biodiversity Hotspots has been questioned and disputed as the most suitable method of prioritising biodiversity and regions for conservation (Kareiva and Marvier, 2003; Orme *et al*., 2005; Marchese, 2015), the substantial overlap with CWR hotspots, CWR distributions and priority *in situ* CWR conservation sites combined with their high profile make Myers' Biodiversity Hotspots a definite candidate for CWR *in situ* conservation. In particular there is significant scope for *in situ* CWR protection in the top 10 priority Biodiversity Hotspots identified here as: Mediterranean Basin, Irano-Anatolian, Caucasus, Tropical Andes, Himalaya, Indo-Burma, Madrean Pine-Oak Woodlands, Mesoamerica, Cerrado and Sundaland. In particular, the Mediterranean basin requires the greatest *in situ* protection with 30 priority sites for CWR conservation being located there, however other hotspots may need more urgent action depending on rates of genetic erosion, habitat loss and level of threat. The CWR found in these hotspots even have the ability to enhance existing projects carried out by Conservation International in these regions. The following are projects run by Conservational International within Biodiversity Hotspots which could be enhanced by CWR *in situ* conservation and utilisation or vice versa (Conservation International, 2016b):

- Sustainable coffee growing in Mexico – Conservational International have been working with a major coffee shop multinational to develop sustainability standards for coffee farming in Mexico, which protect forests from land use change, whilst providing better living standards and incomes for farmers. As suitable land for coffee production is expected to decline up to 40% due to climate change in several countries within the Mesoamerica hotspots (Glen *et al.*, 2013), CWR could benefit this project by reducing the negative effects of climate change by providing climate tolerant traits to new coffee varieties. Coffee CWR conserved *in situ* in Ethiopia and Tanzania, which fall into the Eastern Afromontane, Horn of Africa and Coastal Forests of Eastern Africa could play a major role in maintaining sustainable coffee agriculture in Biodiversity Hotspots and therefore long term protection for forests and farmers livelihoods.

- Indigenous communities protecting forests in Ecuador– this project involves incentivising indigenous communities to protect and sustainably use the forest and the natural capital around them by supplying housing, education, healthcare in return. This is a concept that could be expanded to areas where there are high concentrations of CWR via the establishment of community conserved areas and incentivised using ecosystem service payments. Incorporation of indigenous peoples as guardians of conservation areas has been successfully used for other CWR in the case of wild potatoes in the Parque De La Papa in Peru (Hunter and Heywood, 2011) and could work in the Biodiversity Hotspots.

- Providing insights for African farmers – Conservation International is helping farmers in Tanzania to plan their agriculture better in the face of climate change by monitoring environmental conditions such as precipitation, soil health and temperature through an initiative called Vital Signs. Data from such initiatives can help to identify areas most vulnerable to climate change and which may benefit from growing climate resilient crop varieties developed using CWR genetic diversity. Conserving CWR *in situ* in Biodiversity Hotspots worldwide and making this material available to plant breeders will help to ensure farmers in Africa will have crops that can withstand the particular aspects of climate change affecting those areas. This is particularly vital due to the projected future crop losses in the African continent (Lobell *et al*., 2008, 2011; Nelson *et al*., 2009).

The projects run by Conservation International throughout the Biodiversity Hotspots have strong links to communities and have developed community conserved areas in some regions which would be a valuable resource and framework for CWR *in situ* conservation. The focus on projects involving agriculture, community conserved areas, habitat preservation and ecosystem services within Biodiversity Hotspots indicates that CWR can improve and add resilience to these activities and suggest that Biodiversity Hotspots are a good candidate for furthering CWR *in situ* conservation.

There is also a need tofocus CWR conservation actions beyond Biodiversity Hotspots in areas where CWR hotspots do not overlap, such as eastern USA and mainland Europe. For example, this approach could be applied to WWF Ecoregions such as the Appalachian Forests and Allegheny Highland Forests found in the temperate broadleaf and mixed forests biome in eastern USA where there is no Biodiversity Hotspot. This joined up approach for CWR conservation has the scope to be expanded to other concepts of biodiversity prioritisation such as Centres of Plant Diversity and Key Biodiversity Areas (KBA), like Important Plant Areas (IPA), to improve the profile, awareness and *in situ* conservation of CWR in the wider conservation community and maximise the use of available conservation funds.

CHAPTER 5

A comparison of global crop wild relative hotspots with theories on centres of plant domestication and diversity

This chapter is being prepared for publication as:

Vincent, H. and Maxted, N. (2016) A comparison of global crop wild relative hotspots with theories on centres of plant domestication and diversity (in prep.)

Author contributions:

Conceived and designed the study: **HV**, NM

Data collation and preparation: **HV**

Performed analysis: **HV**

Analysed results: **HV**

Wrote the paper: **HV**

Critically reviewed the paper: **HV**

5.1 Abstract

Plant genetic resources (PGR) are the building blocks for crop diversity. Crop wild relatives (CWR), a subset of PGR, are rich in genetic diversity. With the negative effects of climate change already being felt worldwide and potentially disastrous future projections for crop yields, CWR can be utilised to breed climate resilient crops. As the progenitors and congeneric taxa of domesticated crops, CWR species are often assumed to exist near centres of crop domestication, in fact the CWR community regularly describe Vavilov centres of diversity as being areas of particular CWR richness worldwide, sometimes suggesting conservation efforts should be concentrated there. In this paper we aim to discover the extent to which Vavilov centres and other concepts on crop domestication areas are congruent with areas of high CWR diversity for crops important to food security. We discovered that Vavilov centres had the best overlap with CWR hotspots and distributions in comparison to other crop domestication concepts, however important CWR hotspots in west and east USA, West Africa, South-east Brazil and Europe were not represented.

5.2 Introduction

The transition from hunter-gatherer communities to agriculture first occurred some 10,000 years ago in several independent cradles around the world and continued until as recently as 3000-4000 years ago (Diamond, 2002). Since the mid-19th century scholars have attempted to pinpoint the locations where crop domestication first began, however, exact whereabouts have proven difficult to delimit. Charles Darwin was one of the first to investigate the variability of domesticated species versus wild counterparts illuminating and documenting the processes of inheritance and selection of traits under artificial human direction, substantiated with considerable examples and evidence (Darwin, 1868). Darwin also questioned the location of plant crop originations in this work but concluded it would be extremely difficult to discover the exact centres of domestication; however, one of Darwin's contemporaries took up this challenge. Alphonse de Candolle was a botanist, and one of the first crop geographers, who wrote extensively on the geography and origins of individual cultivated plant species, using historical data, presence of related wild species, variation patterns and archaeological information to determine broad areas of plant domestication. De Candolle combined his research on individual crop species to determine three separate centres of plant crop domestication; the Fertile Crescent, Mesoamerica and South East Asia (de Candolle, 1886). However, the data he had available at the time was imperfect, and combined with his creationist views lead to faulty assumptions in his work.

The next important figure in the history of defining centres of crop origin was Nikolai Ivanovich Vavilov, the father of plant genetic resources conservation and utilisation, who dedicated his life to studying the diversity of plant species and their utilisation for crop improvement in the Soviet Union. Inspired by the work of de Candolle, Vavilov was the first to attempt defining crop domestication areas into more precise locations; in 1926 Vavilov published his theory on the centres of crop origins based upon a study of literature, geography and nomenclature surrounding cultivated plants (Vavilov, 1926). Vavilov initially identified five centres of plant crop origination using a so called differential phytogeographical approach which involved the following steps: (a) delimitation of plants into Linnean species and morphological units; (b) determination of the geographical distribution of these plants in the past; (c) determination of the inherited variation of characteristics of each plant species; (d) definition of geographical areas where there is a wide range of inherited variation in forms, for multiple species (Vavilov, 1992). The five centres were geographically broad and encompassed the Mediterranean, Central and South America, the Far East and South-western Asia. The basic centres formed the foundation and rationale for many of Vavilov's collecting missions. The accumulation of information from a wide study of global plant diversity, collecting missions and an increase in archaeological findings helped Vavilov to refine his centres of crop origin and diversity theory, and increase the number of centres from five to eight, including several sub-regions, important for their wealth of cultivated plant and CWR diversity (Vavilov, 1935). These areas included: the Chinese centre; the Indian centre; the Indo-Malayan sub-centre; the Inner Asiatic centre; the Asia Minor centre; the Mediterranean centre; the Ethiopian centre; the Central American centre; The Peruvian-Ecuadorian-Bolivian centre with sub-centres in both Chiloe, Chile and around the Brazil-Paraguay border. Vavilov once again modified his theory in 1940 by combining the Inner Asia and Asia Minor centres, whilst introducing a new sub-centre around Bogota, Colombia (Vavilov, 1940); the Brazil-Paraguay sub-centre was omitted from this publication for unknown reasons, although Hawkes (1993) suggests it was overlooked accidently during a period of severe personal and professional struggle for Vavilov and should be reinstated.

After Vavilov's premature death, his colleagues continued to develop his centres of crop origin and diversity theory and even today, scientists are still investigating the originations of various crops. Several of the major theories are detailed here.

Zhukovsky, a colleague of Vavilov's, sought to delimit areas of crop diversity and areas of wild species diversity separately (Zhukovsky, 1965). He defined 12 broad areas termed mega gene centres which contained a wealth of domesticated plant diversity (Zeven and Zhukovsky, 1975). The mega centres were based upon Vavilov's centres of diversity theory and showed areas of high crop diversity. Zhukovsky enlarged centres such as the Ethiopian centre to encompass the whole of Africa and included the European and Siberian region along with the whole of Australia. Zhukovsky also described over 100 microgene centres within the mega gene centres which exhibited exceptional local diversity and richness of wild species related to cultivated crops.

Harlan sought to improve on the theories suggested by Vavilov and Zhukovsky, to determine centres and non-centres of agricultural origin using a combination of methods rather than relying heavily on phytogeography techniques as Vavilov did. Harlan also had better data to work with as a great deal of archaeological and plant genetic work had been accomplished since Vavilov's era. Harlan described three main centres in which agriculture developed independently and then spread; the Near East centre, the North Chinese centre and the Mesoamerican centre. Each main centre had a corresponding non-centre to which the ideas of crop domestication spread and were widely utilised leading to a more diffuse spread of domestication and a great variety of forms of crops (Harlan, 1971). The corresponding non-centres are defined as the African non-centre, the Southeast Asian and South Pacific non-centre and the South American non-centre.

Current knowledge of the centres of crop domestication has been greatly increased by the improvements and developments of scientific methods since the time of de Candolle and Vavilov. The advancements in molecular biology and archaeobotany, combined with an increase in the number of physical archaeological sites discovered with samples of ancient crops have led to a more thorough definition of the area of domestication for individual crops. Puruggnan and Fuller (2009) summarise current collective knowledge on the areas of domestication for various major crops worldwide and describe 25 centres where domestication of various crops began.

PGR are the building blocks for crop diversity. CWR, a subset of PGR, are the wild and weedy relations of domesticated crops, including progenitors. CWR have been increasingly and successfully used as gene donors for improving crops for over the last 60 years (Haijar and Hodgkin, 2007; Maxted and Kell, 2009). With the negative effects of climate change already being felt worldwide and potentially disastrous future projections for crop yields (Lobell *et al.*, 2008; Porter *et al.*, 2014; Challinor *et al.*, 2016), plant breeders are calling for greater diversity of plant genetic resources and CWR to breed climate resilient crops (McCouch *et al.*, 2013). As the progenitors and congeneric taxa of domesticated crops, CWR species are often assumed to exist near centres of crop domestication; in particular the CWR community often describe Vavilov centres of diversity as being areas of particular CWR richness worldwide, sometimes suggesting conservation efforts should be concentrated there (Rubenstein *et al.*, 2005; Maxted and Kell, 2009; Stolten *et al.*, 2010; Ford-Lloyd *et al.*, 2011; Kell *et al.*, 2015). However, the spatial relationship between CWR of major crops for food security and Vavilov centres of diversity has yet to be examined as a whole. In this paper we aim to discover the extent to which Vavilov centres of diversity are congruent with areas of high CWR diversity for crops important to food security and farmer income provision and whether there are any significant CWR hotspots found outside the centres and discuss the implications for CWR conservation. Furthermore, we examine whether other concepts of crop domestication and diversity centres offer a better fit with regard to CWR hotspots and species distributions over Vavilov centres of diversity.

5.3 Methods

5.3.1 Target CWR and occurrence data collation

Crops important for food security and farmer income provision were identified for inclusion in the analysis by consulting the Harlan and de Wet CWR Inventory (Vincent *et al.*, 2013). Similarly, their closely related CWR (those in gene pool (GP) 1B or GP2; or, taxon group (TG) 1B-3) and those that had previously been used in/had potential for crop breeding were defined as target taxa using the Harlan and de Wet CWR Inventory and the GRIN Global CWR Portal (GRIN Global, 2015). Closely related taxa were identified using the gene pool concept developed by Harlan and de Wet (1971) to categorise wild species based upon their genetic relationship to crops; GP1B CWR are those that are closely related and easily hybridise with the crop including con-specific and progenitor CWR, and GP2 CWR are those which can hybridise with crops to produce partially fertile offspring but crossing is often difficult using conventional methods. The taxon group concept is applied when hybridisation information between CWR and crop is lacking, therefore using taxonomic classification as a proxy for genetic relatedness (Maxted *et al.*, 2006); TG1B CWR equate to taxa in the same species as the crop, TG2 equates to CWR in the same series or section as the crop and TG3 relates to CWR in the same subgenus as the crop.

In order to model the distributions of target CWR species, occurrence records were downloaded from a major repository of geo-referenced CWR data (Castañeda-Álvarez *et al.,* 2016) and edited to remove: cultivated taxa and occurrences, occurrences outside of taxon native range, non-target taxa and occurrences with no coordinates or inaccurate coordinates (where coordinates have greater than 10 km potential inaccuracy). Target CWR were recorded at the species level due to identification inconsistencies at the subordinate taxa level and the poor number of occurrence records for many sub-taxa. Species nomenclature was revised to match that of GRIN (GRIN Global, 2015) and species native ranges were obtained from the Harlan and de Wet Inventory (Vincent *et al.*, 2013).

5.3.2 CWR species distribution modelling

To maximise the use of small sets of occurrence records per species and overcome the effects of uneven, unrepresentative sampling across species native ranges, species distribution modelling was used to predict potential CWR distributions. MaxEnt software (version 3.3.3a) was used to model species potential distributions due to it being considered the best algorithm for producing accurate predictive distribution maps with presence only data (Elith and Leathwick, 2009). Only species with 10 or more unique occurrence records were modelled using MaxEnt (Ramírez-Villegas *et al.*, 2010).

To measure suitability of habitat for modelled species and produce quality predictions, MaxEnt requires environmental variables, occurrence points and background points from the species native area (Phillips *et al.,* 2006). Twenty seven variables were chosen as potential inputs for MaxEnt modelling and were subjected to stepwise variance inflation factor (VIF) analysis to remove collinear variables based upon variable values obtained from occurrences of each CWR (Merow *et al.*, 2013). Variables with a collinear threshold value of 10 or more were removed from the total set. Variables included bioclimatic variables obtained from the Worldclim database (Hijmans *et al.*, 2005), altitude and seven major soil factors from the ISRIC World Soil Information database (Hengl *et al.*, 2014) (Supplementary Table 3.1). Modelling was performed at the 2.5 arc minutes resolution (~5km at the equator), using

10,000 random background points from each species native range to train models. MaxEnt was performed using a five-fold cross validation technique and models were projected onto the native range of the species. The criteria proposed by Ramírez-Villegas *et al.* (2010) were applied to each predictive CWR distribution model to test their validity; (a) the five-fold average of the test Area Under the Test of the Receiver Operating Characteristic (ROC) curve (ATAUC) was greater than 0.7, (b) the standard deviation of the ATAUC for the individual five individual folds was lower than 0.15, and, (c) the proportion of the predicted distribution where the standard deviation was greater than 0.15 was less than 10% of the total predicted distribution. For valid models, presence/absence maps were created per species by applying the maximum training sensitivity plus specificity (MAXTRSS) logistic threshold to the logistic values generated across the native range (Liu *et al.*, 2013). For CWR that produced invalid models or had fewer than 10 unique records, potential distributions were approximated using a 50 km circular buffer around each species occurrence (Hijmans *et al.,* 2001).

5.3.3 Creation of centres of crop domestication and diversity spatial data

To assess the congruence of centres of crop domestication and diversity with CWR distributions and hotspots, it was necessary to create spatial polygon data from centres of crop domestication and diversity maps in the literature for use in GIS. Four concepts were chosen for comparison with CWR hotpots and distributions: Vavilov centres of diversity (Vavilov, 1935, 1940), Zeven and Zhukovsky's mega gene centres (Zeven and Zhukovsky, 1975), Harlan's centres and non-centres of crop domestication (Harlan, 1971) and current knowledge on crop domestication areas as collated and mapped by Puruggnan and Fuller (2009). Shapefile polygons of each centre within the four concepts were drawn matching the original maps of the four concepts, using the GIS software QGIS, version 'Essen' and validated to ensure polygons were not self-intersecting or unclosed. The individual centre shapefiles from each concept were then rasterised to a grid of 5 arc minutes resolution (~10 km at the equator) to enable comparison with CWR hotspots and CWR distributions, which were represented by rasters of the same resolution.

5.3.4 Assessing congruence of CWR hotspots and distributions with centres of crop domestication and diversity

To assess how well the Vavilov centres of diversity and the three other concepts on crop domestication and diversity correspond to CWR distributions and areas of particular high CWR richness, a global raster defining CWR hotspots was obtained from Vincent *et al.* (Chapter 4 this thesis). The CWR hotspots were delineated using a species richness map as input for the Getis-Ord Gi* statistic which measures whether the observed values in cells (in this case, number of unique CWR species) are significantly different from expected values under the null hypothesis of complete spatial randomness (CSR) (Vincent *et al.*, Chapter 4 this thesis). Pairwise similarity between each concept and CWR hotspots was explored using Jaccard's coefficient which is defined as A/(A + B + C), where A represents grid cells present in both concept and CWR hotspots rasters, and B and C represent grid cells present in only one of the respective rasters. Jaccard's coefficient was also calculated for each individual centre in the concepts and CWR hotspots. Percentage coverage between CWR hotspots and individual centres within concepts on crop domestication and diversity, as well as each concept as a whole, was calculated by overlaying rasters in R (R Core Team, 2015). Additionally, numbers of CWR potential distributions located within individual centres and total concepts were obtained. Concepts were ranked based upon three criteria to identify those best representing the distributions and hotspots of CWR for crops important for food security and farmer income. The rankings were: (a) highest to lowest percentage of CWR hotspots area overlapping concepts, (b) highest to lowest percentage of concept area overlapping CWR hotspots, and, (c) highest to lowest number of unique CWR potential distributions within concepts.

5.4 Results

A total of 1425 CWR were identified as being closely related to or important for crop breeding to 167 crops that significantly contribute to human food security and farmer income provision. The 1425 CWR were comprised of 236 GP1B species; 675 GP2 species; 30 TG1B species; 154 TG3 species; 103 species with confirmed breeding use, and, 67 species with potential use in crop breeding. The downloaded CWR occurrence dataset was edited and reduced down from over 5 million total records to 334,527 good quality records. Occurrence records with good quality co-ordinate data were unavailable for 164 of the target CWR species; therefore only 1261 priority CWR could be included in the analysis. Furthermore, 470 species were poorly represented in the dataset with fewer than 10 unique records each. In total 791 CWR species potential distributions were successfully modelled using MaxEnt, with the remaining 470 CWR modelled using the 50 km circular buffer method.

The GIS polygon representations of the four centres of diversity and domestication were drawn in QGIS, version ‘Essen’, and are shown in Figure 5.1. The four concepts on centres of crop domestication and diversity are broadly different, both in terms of numbers of centres, their exact location and size. Indeed, the largest concept, suggested by Zeven and Zhukovsky

(1975) is 561.49% larger than the concept with the smallest area – that of Puruggnan and Fuller (2009). Puruggnan and Fuller (2009) have delimited the most individual centres with 25, followed by Vavilov (1935, 1940) and Zeven and Zhukovsky (1975) with 12 each, and lastly, Harlan (1971) has described the fewest with six.

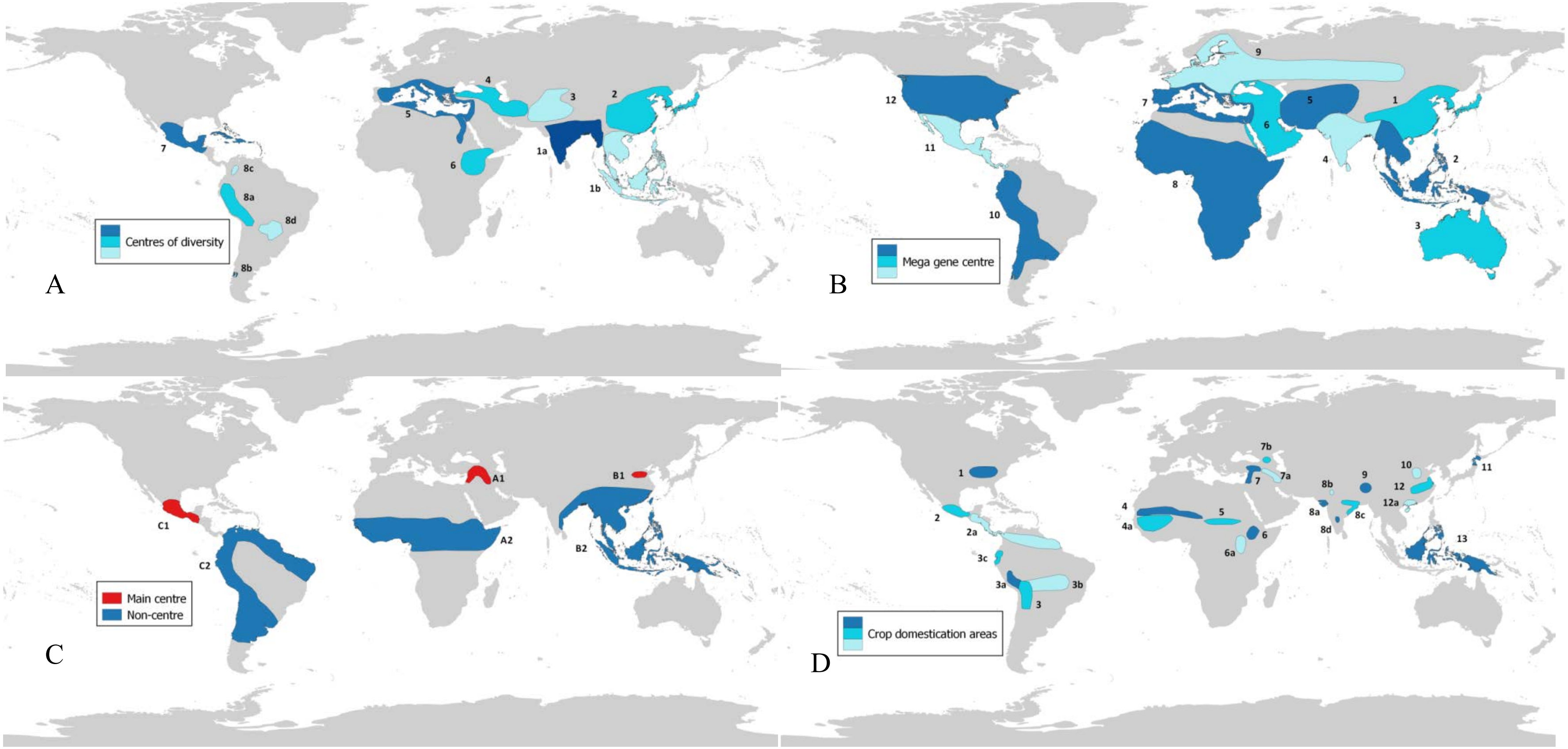

Figure 5.1 Centres of crop domestication and diversity: (A) Vavilov centres of crop diversity (Vavilov, 1935, 1940; Hawkes, 1993); (B) mega gene centres of cultivated plants (Zeven and Zhukovsky, 1975); (C) centres and non-centres of agricultural origin (Harlan, 1971); and, (D) current knowledge on crop domestication areas (Purugganan and Fuller, 2009)

To assess the congruence between concepts on centres of crop domestication and diversity and CWR hotspots, pairwise similarity of each concept with CWR hotspots and total number of CWR was measured (Table 5.1). In terms of percentage coverage of CWR hotspots, the Zeven and Zhukovsky mega gene centres as a whole contain the highest proportion of hotspots with 92.71%, followed by Vavilov centres of diversity with 49.02%, Harlan centres and non-centres with 20.25% and lastly, Puruggnan and Fuller crop domestication areas with 11.99% CWR hotspot coverage. Furthermore, Jaccard's Similarity Index calculated for concepts and CWR hotspots shows that as a whole the Vavilov centres of diversity have the greatest similarity to CWR hotspots with a value of 0.20, followed by the Zeven and Zhukovsky mega gene centres with an index value of 0.13, the Harlan centres and non centres with 0.07 and Puruggnan and Fuller crop domestication areas with a value of 0.06 (Table 5.1). In regard to the percentage of total CWR species within centres of domestication and diversity, Zeven and Zhukovsky mega gene centres again contain the highest proportion with 1161 species (92.07% of total CWR) from 164 crops, followed by Vavilov centres of diversity with 910 species (72.16% of total CWR) from 162 crops, Harlan centres and non-centres with 789 species (62.57% of total CWR) from 150 crops and finally, Puruggnan and Fuller crop domestication areas with 771 species (61.14% of total CWR) from 155 crops.

Table 5.1 Number of CWR and crops per concept, percentage of CWR hotspots area coincident to each concept and Jaccard’s similarity Index between CWR hotspots and individual concepts.

Concept	**Number of CWR**	**Number of crops**	**Percentage of CWR hotspots area coincident with each concept**	**Jaccard’s similarity Index between concepts and CWR hotspots**
Vavilov	910	162	49.02	0.20
Zeven and Zhukovsky	1161	164	92.17	0.13
Harlan	789	150	20.25	0.07
Puruggnan and Fuller	771	155	11.99	0.06

CWR hotspots overlap to different degrees with the four concepts of crop domestication and diversity as evidenced in Figure 5.2. The percentage of total CWR hotspot cells overlapping no concepts of domestication and diversity was 5.72%, the percentage of CWR hotspots overlapping one concept 39.57%, the percentage of CWR hotspots overlapping two concepts was 34.58%, the percentage of CWR hotspots overlapping three concepts was 15.29% and the percentage of CWR hotspots overlapping all four concepts was 4.84%. The areas with greatest agreement between concepts on crop domestication and diversity in regard to CWR hotspots coverage were located in Central America, the Fertile Crescent, a fraction of the Andes region, southern Philippines, Borneo, the small CWR hotspot in Ethiopia, southern China and Sulawesi. CWR hotspot areas such as mainland Europe, western USA, northern Australia and eastern Brazil have only one overlapping concept; further areas in eastern

Brazil, the UK and Morocco have no overlap with concepts on crop domestication and diversity.

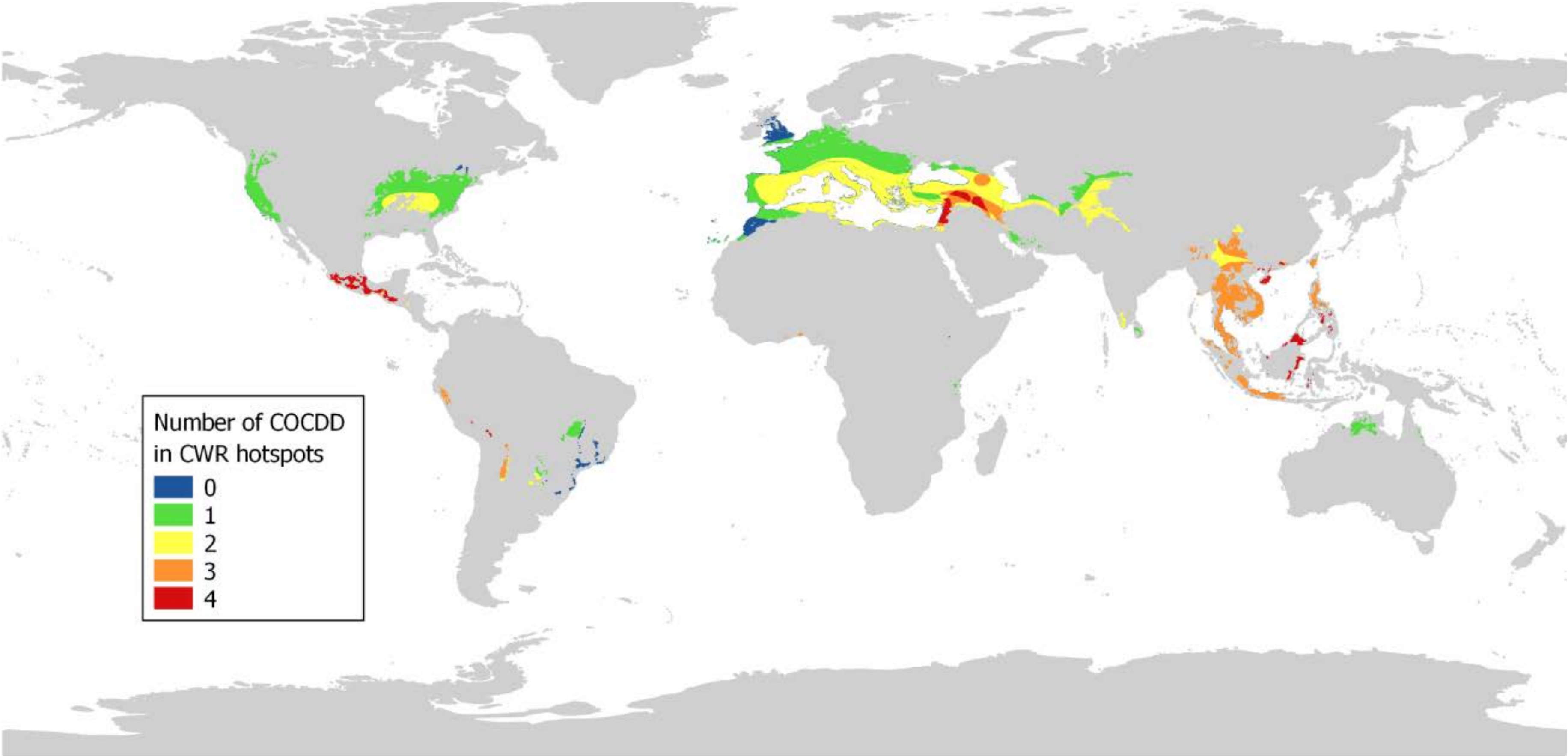

Figure 5.2 Number of concepts on crop domestication and diversity (COCDD) overlapping CWR hotspots

Figure 5.3 shows the CWR hotspot, CWR species and related crop coverage of every individual centre in each concept of domestication and diversity. The Vavilov centres with greatest overlap with CWR hotspots were centres five (the Mediterranean) and four (Inner Asia), with 75.00% and 61.65% respectively. The centres with no or poor overlap were 8b, 8c, 8d, and six. Centre five has the greatest number of total CWR with 279, followed by centre four with 219, and 1b with 184 CWR. Centre 8b contained the fewest CWR species with only two. Centre three had the greatest diversity of related crops with 79, closely followed by centres five and four with 78 and 77 respectively.

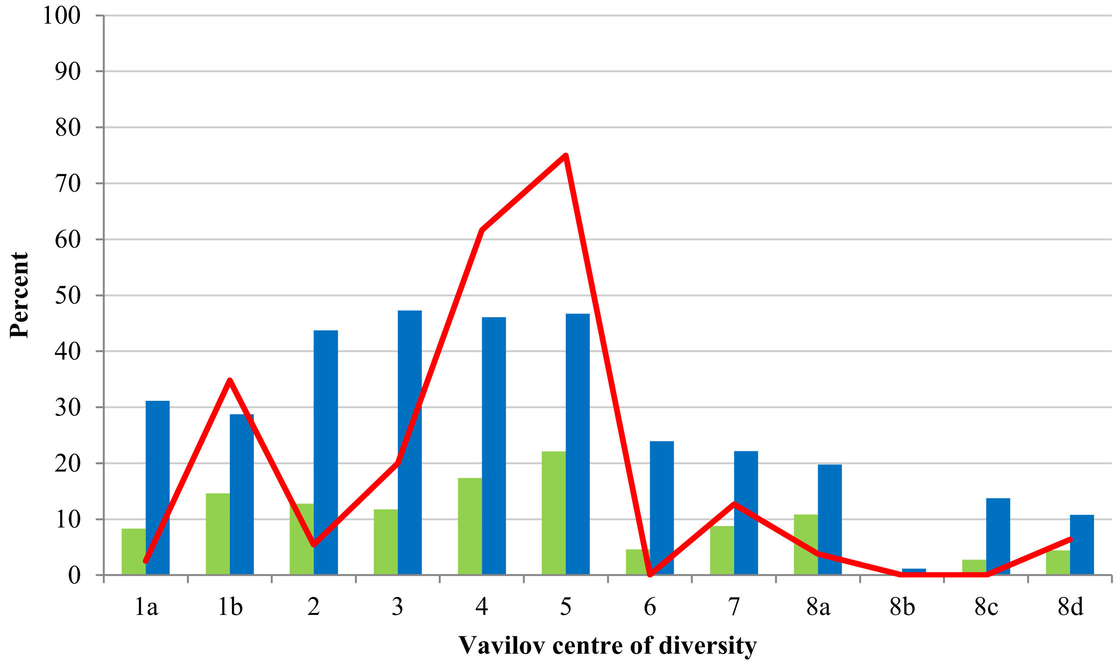

Figure 5.3 Percentage overlap with CWR hotspots, percentage of total CWR species and percentage of total related crops per Vavilov centre of diversity. The green bar = percentage of total CWR per centre, the blue bar = percentage of total related crops per centre and red line = centre overlap with CWR hotspots (%)

The Zeven and Zhukovsky mega gene centres exhibit similar levels of CWR species representation individually to Vavilov centres; however contain greater numbers of related crops (Figure 5.4). The centre with the greatest overlap with CWR hotspots was centre seven (the Mediterranean) with 69.25%, followed by centre two (East Asia) with 29.85% coverage. Centres with the least overlap were centre eight (Africa) and centre three (Australia). Centres containing the most CWR species were: seven with 279 CWR, six with 240 and two with 228 CWR. The fewest were contained in centre three, with 43 CWR. The greatest number of related crops was found in centre six with 85, closely followed by centre five with 84 crops.

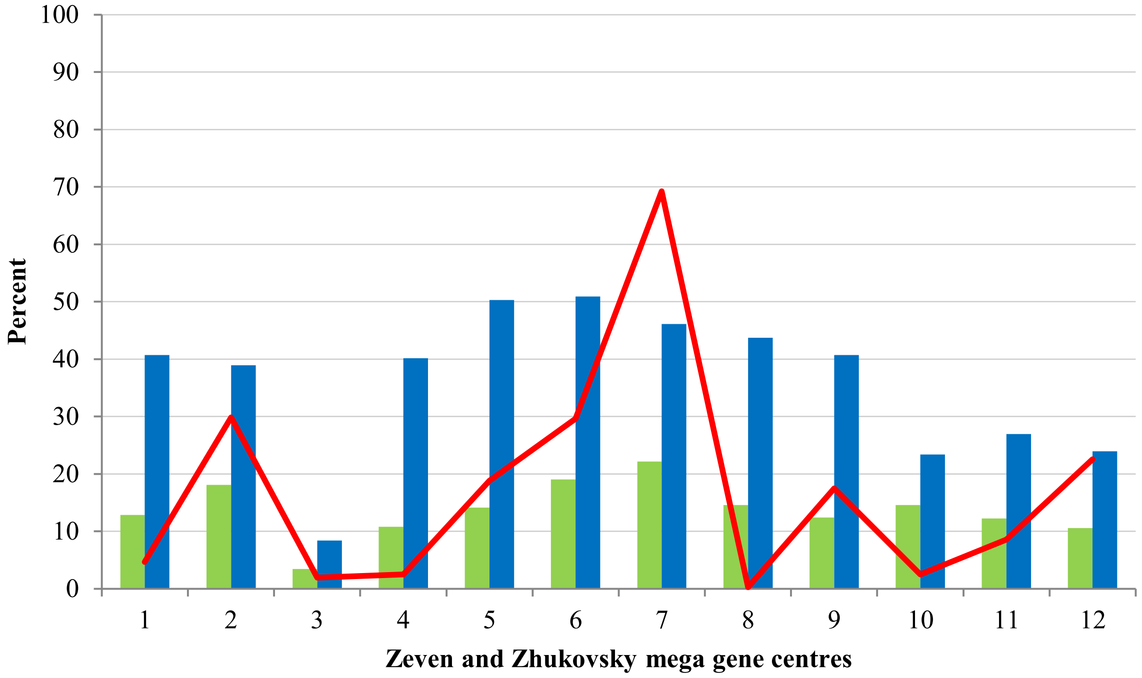

Figure 5.4 Percentage overlap with CWR hotspots, percentage of total CWR species and percentage of total related crops per Zeven and Zhukovsky mega gene centre. The green bar = percentage of total CWR per centre, the blue bar = percentage of total related crops per centre and red line = centre overlap with CWR hotspots (%)

The Harlan centres and non-centres have poor intersection with CWR hotspots, except for the centre in the Fertile Crescent (Figure 5.5). They also contain low numbers of CWR species and related crops in comparison to Vavilov and Zeven and Zhukovsky centres. The Harlan centre with the greatest overlap with CWR hotspots was A1 (Fertile Crescent) with 63.65%, followed by C1 (Mesoamerica) with 24.95%. Centres B1 and A2 had no or very poor coincidence with CWR hotspots. The centre with the greatest number of CWR species was B2 with 260 CWR, followed by A1 with 205 CWR; centres B1 and A2 had the fewest CWR with 19 and 81 respectively. Centre A1 has the greatest diversity of related crops with 72, followed by B2 with 68; B1 had the fewest related crops with 18.

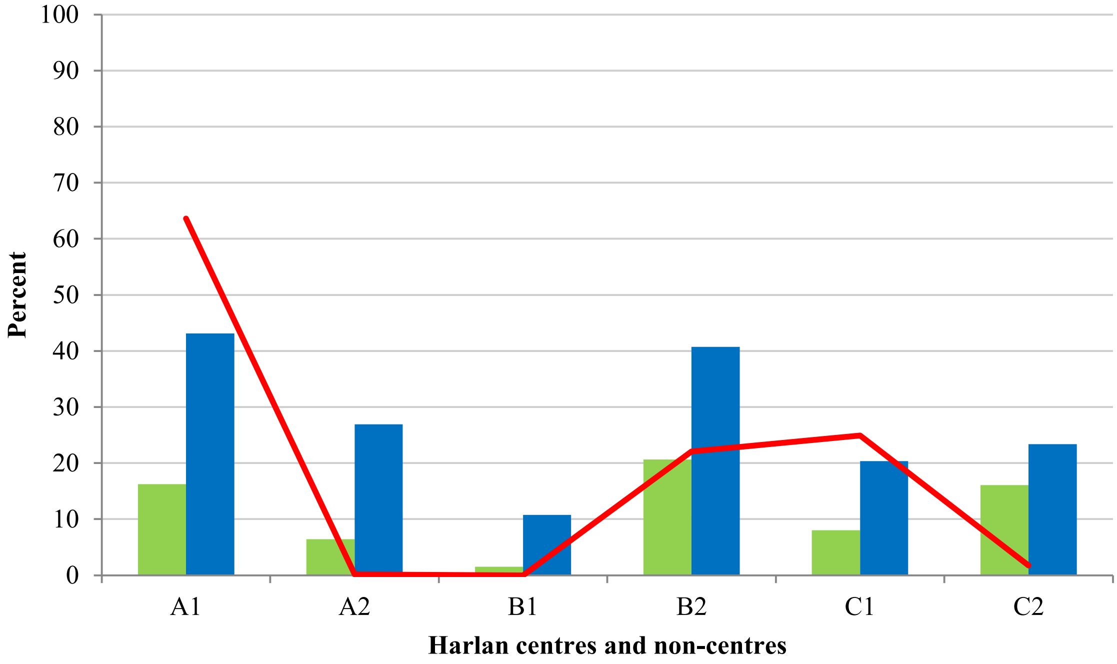

Figure 5.5 Percentage overlap with CWR hotspots, percentage of total CWR species and percentage of total related crops per Harlan centre and non-centre. The green bar = percentage of total CWR per centre, the blue bar = percentage of total related crops per centre and red line = centre overlap with CWR hotspots (%)

Puruggnan and Fuller centres of crop domestication have greater overlap with CWR hotspots than the centres in the three other concepts (Figure 5.6); however, the number of CWR species in each individual centre is much lower than all of the other concepts. In terms of number of related crops, the Puruggnan and Fuller centres are at a similar level to the Harlan centres and non-centres (Figure 5.5). Centre 7b has 100% overlap with CWR hotspots, followed by centre seven with 88.26% and 7a with 76.13%; however, 12 further centres had no overlap at all with CWR hotspots. Centre seven had the greatest number of CWR species with 194, followed by centre 7a with 127 and centre 13 with 103 CWR. Centre four had the fewest CWR with eight. Centre seven also had the greatest diversity of related crops with 67, followed by 7b with 54 and 7a with 53; the centres with the fewest crops were centre four and centre 8b, with six and eight crops respectively.

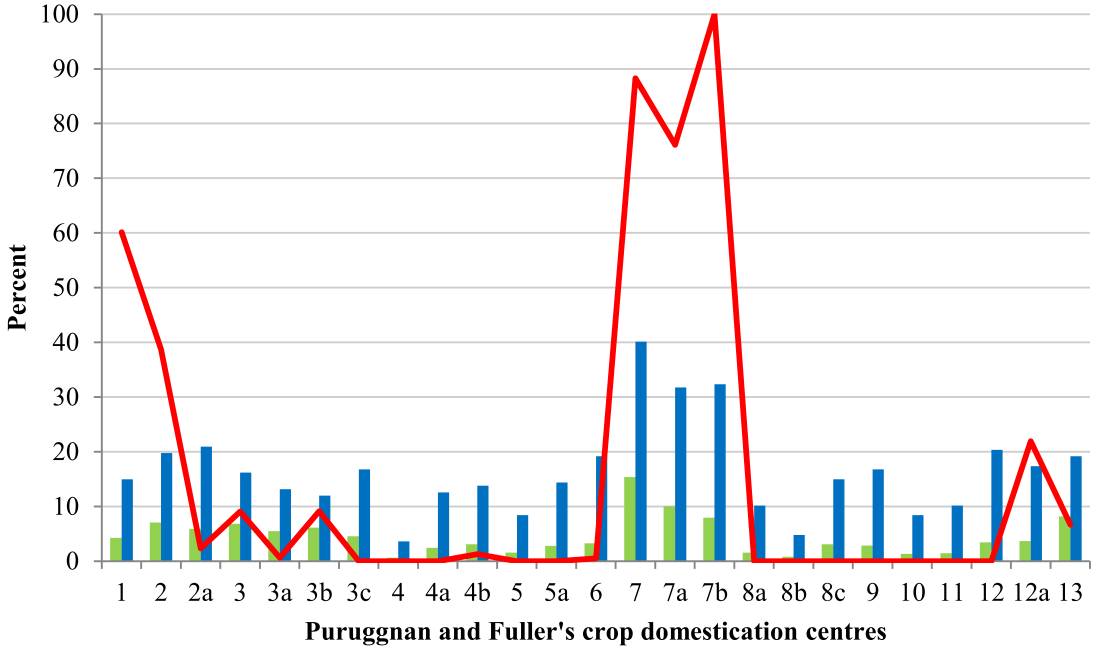

Figure 5.6 Percentage overlap with CWR hotspots, percentage of total CWR species and percentage of total related crops per Puruggnan and Fuller crop domestication centre. The green bar = percentage of total CWR per centre, the blue bar = percentage of total related crops per centre and red line = centre overlap with CWR hotspots (%)

Table 5.2 shows the rankings of each of the four concepts on centres of crop domestication and diversity. Rankings show that the Zeven and Zhukovsky mega gene centres (two first place rankings, one second, and one fourth) and Vavilov centres of diversity (three second place rankings and one first place ranking) concepts are the consistently top ranked out of the four, in regard to CWR hotspots and CWR distribution coverage. Vavilov centres were found to have 25.32% of their total combined area overlapping with CWR hotspots, over 10% more than the Zeven and Zhukovsky mega gene centres; Harlan centres had the least area congruent with CWR hotspots with only 9.50%. Puruggnan and Fuller centres were found to have the highest number of CWR per concept area, with 339.28% more CWR per concept area than the vast Zeven and Zhukovsky centres; Puruggnan and Fuller centres also contain 56.24% more CWR per concept area than the next nearest ranked concept, the Vavilov centres of diversity.

Table 5.2 Rankings for concepts on centres of crop domestication and diversity and their overlap with CWR hotspots and CWR distributions.

Rank	Concept containing the most CWR hotspots	Concept with highest percentage of area covered by CWR hotspots	Concept with highest number of CWR	Concept with highest number of CWR divided by concept area
1	Zeven and Zhukovsky	Vavilov	Zeven and Zhukovsky	Puruggnan and Fuller
2	Vavilov	Zeven and Zhukovsky	Vavilov	Vavilov
3	Harlan	Puruggnan and Fuller	Harlan	Harlan
4	Puruggnan and Fuller	Harlan	Puruggnan and Fuller	Zeven and Zhukovsky

5.5 Discussion

Plant genetic resources, in particular CWR, are a vast underutilised source of genetic diversity that can be utilised by plant breeders to make more nutritious, higher yielding, input efficient, pest and disease tolerant and climate resilient crop varieties (Warschefsky *et al.*, 2014; Redden, 2015). However, CWR are under-conserved thus preventing breeders from accessing a wider range of genetic resources (McCouch *et al.*, 2013) and threatened in the wild, jeopardising the future of CWR genetic diversity and its potential use in breeding (Kell *et al.*, 2012). Throughout the literature on CWR conservation, it is often remarked that Vavilov centres of diversity are coincident with areas of high CWR diversity (Rubenstein *et al.*, 2005; Maxted and Kell, 2009; Stolten *et al.*, 2010; Ford-Lloyd *et al.*, 2011; Hummer and Hancock, 2015; Kell *et al.*, 2015). In this paper we examined the validity of this hypothesis by examining whether the hotspots and distributions of 1261 CWR related to 167 crops important for food security and income provision were indeed analogous with Vavilov centres of diversity. We further investigated whether other theories on areas of crop domestication and diversity were congruent with CWR and to what extent.

The results indicate that unsurprisingly, all four concepts have some overlap with CWR hotspots and individual distributions. Zeven and Zhukovsky mega gene centres have the greatest overlap with CWR diversity, most likely due to the fact they cover more of the terrestrial world than the other concepts. In fact, the combined total area of the other three concepts is still less than the area covered by Zeven and Zhukovsky. This leads us to believe that these centres are too extensive and imprecise to correctly determine CWR hotspots and distributions. Harlan centres and non-centres appear to have the poorest fit with CWR hotspots and distributions, with no centres located in the Mediterranean basin, Europe or Central Asia where there is strong CWR hotspots presence. In this study, Puruggnan and Fuller offer the most recent information on areas of crop domestication; therefore they are more compact, well-defined and specific in comparison to the relatively large areas defined in the other concepts. Although there is significant overlap with CWR hotspots for some centres identified by Puruggnan and Fuller, such as those in the Caucasus and Fertile Crescent, 12 centres contained no CWR hotspots and six of those contained fewer than 20 CWR species. Furthermore, the major CWR hotspots in the Mediterranean and Europe are not represented. Vavilov centres of diversity are consistently placed in the top two highest rankings for CWR hotspot and distribution congruence and had the largest Jaccard's Similarity Index out of all concepts, making them the best fitting concept studied here in regards to CWR. However, Vavilov centres of diversity do not coincide with all CWR hotspots worldwide. Important areas such as eastern USA, the west coast of USA, west Africa and eastern South America were overlooked by Vavilov but contain a great deal of CWR diversity with sunflower, grape, currants and fruit tree CWR in the USA and CWR from sesame, finger millet, coffee, various yams and *Vigna* Savi beans in West Africa. It is unclear why Vavilov would have discounted these regions, but it could be due to the way he tried to delimit areas of the world by combining two separate objectives – origins of domestication and diversity of crops – which are not analogous. Since Vavilov's era the eastern USA and West Africa regions have been widely accepted as rich areas of diversity for CWR and crops (Harlan, 1992; Puruggnan and Fuller, 2009; Jain and Kharkwal, 2012). Some examples of CWR conservation and CWR research organisations within CWR hotspot regions not covered by Vavilov include the AfricaRice genebank and research centre in Benin and the International Institution for

Tropical Agriculture which has a genebank in Nigeria and research stations throughout West Africa. Furthermore, in eastern USA the wild relatives of cranberry found within national forests are being studied in order to determine key populations to conserve *in situ* (USDA, 2014). The Inner Asian, Mesoamerican, Central Asian and Indo-Malay Vavilov centres particularly correlate with CWR hotspots, however, the Chiloe centre contains very little CWR diversity. The choice of CWR and crops used in this study could have affected the resulting congruence between CWR diversity and concepts on crop domestication and diversity. For example Vavilov studied a great deal more crops than we considered, not just those for food and agriculture, but for industrial and medicinal uses too, which could have had a substantial influence on his delimitation of diverse regions. Also in this study we considered only CWR that are in GP1B–2, TG1B–3 and those that have potential or known use in breeding; it is not clear how Vavilov identified CWR for inclusion in his theories, thus leading to possible inconsistencies. Additionally we only considered CWR from crops that are important to current agriculture; however as diets worldwide have become increasingly homogenous we now rely on a contracted diversity of plant crops (Khoury *et al.*, 2014), significantly fewer than the time of Vavilov. Therefore his research would have been based upon a much broader range of wild genetic diversity than we have studied, potentially under-estimating the congruence between Vavilov centres and CWR diversity worldwide. Another limitation of our study is the use of SDMs. Whilst environmental niche modelling is a useful tool for predicting distributions when occurrence records do not represent the whole species range, it can also over fit causing inflated potential representation of individual CWR distributions, thus affecting the location of CWR hotspots.

In conclusion, all of the concepts have some overlap with CWR diversity, however the most up to date knowledge on crop domestication areas, whilst overlapping CWR hotspot regions no other concept does, is too specific to be analogous to CWR, which seem to have greater spread and range beyond areas of domestication. Conversely the mega gene centres identified by Zeven and Zhukovsky are too vast and non-specific, so whilst covering much CWR diversity it would be difficult to focus CWR conservation on such large areas. Harlan centres and non-centres poorly represent CWR diversity globally due to a lack of centres, particularly in Central Asia, the Mediterranean basin and Europe. Vavilov centres of diversity are the most spatially similar concept to CWR hotspots, making them a reasonable proxy for CWR species diversity; however areas such as Europe, east and west USA, West Africa and eastern South America are overlooked and should be given equal attention when planning for conservation inside CWR rich areas and developing conservation strategies inside Vavilov centres of diversity.

CHAPTER 6

General Discussion

6.1 Overview

The research presented in this thesis has helped to fulfil the first steps in systematic conservation planning for the global conservation of priority CWR. The identification of priority CWR species and development of the Harlan and de Wet CWR Inventory has already had a strong impact on the conservation community, being utilised in a global *ex situ* gap analysis, high profile *ex situ* collecting strategies and numerous national strategies (Khoury *et al.*, 2013; Dempewolf *et al.*, 2013; Landucci *et al.*, 2014; Phillips *et al.*, 2014; Fielder *et al.*, 2015; Kell *et al.*, 2015; Castañeda-Álvarez *et al.,* 2016a). The thesis further builds on this knowledge by presenting the first CWR *in situ* gap analysis of all priority CWR for crops important for food security and using reserve planning to identify preliminary sites for the formation of a global network of *in situ* CWR reserves. Finally, practical methods are explored for the implementation of *in situ* gap analysis recommendations within areas designated as important for biodiversity conservation and areas historically known for PGR diversity, whilst promoting a complementary approach with coincident biodiversity.

A prioritised crop wild relative inventory to help underpin global food security (Chapter 2)

To begin systematic conservation of CWR, it was first necessary to identify which CWR were priorities for increasing food security via their utility for crop breeding. CWR were identified as priorities for conservation globally by using the gene pool and taxon group methods to assess relatedness between crop and CWR. Additional information was collected about each CWR, such as native range, synonyms, history of use in crop breeding and seed storage behaviour. The inventory was made available online for the benefit of the CWR community and conservation planners.

The inventory originally contained 1667 taxa, divided between 37 families, 108 genera, 1392 species and 299 sub-specific taxa and now contains over 2400 taxa after various updates. The inventory is well used, particularly at the European level where it has been promoted as a valuable tool for national inventories and strategies. However, one area which could improve the inventory is the clarification of genetic relationships within crops gene pools that are currently represented by taxon group and provisional gene pool concepts, for example citrus fruits and tropical fruits such as mango and breadfruit. There is also great scope for adding in more crops and their gene pools into the inventory to further conservation efforts of more minor, but nonetheless important crop gene pools.

Global priorities for *in situ* conservation of wild plant genetic resources: towards the establishment of a global network of crop wild relative reserves (Chapter 3), and, An approach for *in situ* gap analysis and conservation planning on a global scale (Appendix 1)

There are very few *in situ* CWR reserves worldwide (Maxted and Kell, 2009), and the ones that do exist do not meet the genetic reserve standards created by Iriondo *et al.* (2012). The work presented in Chapter 3 and Appendix 1 aimed to address the paucity of *in situ* conservation action globally by providing an in-depth methodology for CWR *in situ* conservation planning at the global level as an exemplar. Additionally, *in situ* gap analysis was carried out to measure the current passive conservation of priority CWR and their genetic diversity in the existing protected area network, and strategies were suggested to form a global network of CWR reserves, maximising genetic diversity coverage and sites identified as potentially climate change resistant. The analysis was run on 1261 CWR chosen for their potential and known utility to crop breeding. The results showed that CWR distribution models were well represented in the existing protected area network, but that 85 CWR were vulnerable to climate change, with expected losses of at least 50% of their current distributions. Reserve planning software was used to select sites worldwide which would maximise genetic diversity and CWR species coverage and protected area coverage. The resulting sites were prioritised based upon richness of CWR and complementarity, producing a priority set of 150 sites worldwide containing 829 CWR.

The next step for continuing this work is the involvement of conservation bodies and stakeholders and ground truthing the 150 priority sites identified in the research, to ensure the CWR do exist where predicted. Additionally, more in-depth results can be obtained from conservation planning by collecting more occurrence data, particularly for CWR with fewer than 10 unique occurrences, crowd sourcing data could be an interesting future prospect here for gaining more occurrence sightings. Further reserve planning with land costs, threat layers and Red List assessments would greatly improve the realism and long term validity of selected sites, and would most likely be required once stakeholders have had their input. There is also a need to factor in no go zones, and areas where conservation implementation would be extremely difficult in reserve planning software; for example along country/political borders and regions where there is warfare, a current example is Syria (Hammill *et al.*, 2016). The speed at which biotechnological techniques are developing and their reduction in costs will no doubt become an invaluable resource to the CWR community in mitigating for climate change and a growing population (Henry, 2014; Brozynska *et al.*, 2016). The genetic diversity data which will be available through projects such as DIVSEEK (www.divseek.org) and other mass sequencing projects can be included in future iterations of reserve planning to ensure genetic diversity representativeness across the CWR *in situ* network (McCouch *et al.*, 2013;

Brozynska *et al.*, 2016). Further study will also be required to fully assess the effects climate change will have on CWR populations *in situ*, this will include field studies and monitoring of populations to record any genetic erosion. Studies into how plant strategies for coping with climate change such as phenotypic plasticity, migration, evolutionary adaptation and even assisted migration implementation will effect long term CWR strategies *in situ* are also required (Nicotra *et al.*, 2010).

To effectively manage a CWR *in situ* network there will need to be a framework established for the monitoring and implementation of conservation at selected sites and decisions will need to be made on who will be responsible for maintaining the sites and how the global network will fit into CWR conservation initiatives and policy at the regional, national and local levels (Maxted *et al.,* 2016).

The legitimacy of protected areas for conserving CWR long term has been questioned, due to some CWR preferring ruderal habitats, the increasing threats affecting protected areas (Mascia and Pailler, 2011; WWF, 2016), lack of funding and adequate management (Leverington *et al.,* 2010), and the lack of plasticity in protected area boundaries in regard to climate change induced plant migration from protected areas (Araújo *et al.*, 2004). This suggests that further work should be carried out to assess possibilities of conserving CWR in less formalised ways such as other effective area-based conservation measures (OECMs) which are being explored by the IUCN, Indigenous peoples' and community conserved territories and areas (ICCAs), areas of shared governance and sustainable use, private protected areas, and disturbed areas such as roadsides or field margins (Jonas *et al.,* 2014; Jarvis *et al.*, 2015; Maxted *et al.*, 2016).

A comparison of crop wild relative hotspots with biologically and ecologically important geographical regions; a case study with Myers' biodiversity hotspots (Chapter 4)

To maximise available funds for conservation Chapter 4 explored how CWR conservation could be promoted and integrated into existing conservation actions in areas of coincident high biodiversity. Global CWR hotspots were created using a species richness map and the Getis-Ord Gi* statistic in ArcMap 10.2. Polygon vector data representing Myers' Biodiversity Hotspots was overlaid with CWR hotspots and predicted distribution models of all assessable CWR to examine whether CWR diversity was congruent with areas of high endemism and exceptional threat. Biodiversity hotspots as a whole had significant overlap with CWR hotspots with the highest coincidence in the Mediterranean basin (91.28%) and the California Floristic Province (90.96%). Overall, there was substantial overlap with Biodiversity Hotspots suggesting they would be good candidates for CWR *in situ* conservation. The priority Biodiversity Hotspots for incorporating CWR conservation were: the Mediterranean Basin, Irano-Anatolian, Caucasus, Tropical Andes, Himalaya, Indo-Burma, Madrean Pine-Oak Woodlands, Mesoamerica, Cerrado and Sundaland.

Future work in this area will include ground truthing of CWR existence in Biodiversity Hotspots and workshops between conservation agencies and the CWR community to discuss how CWR can be included in projects run in the Hotspots and how to maintain the conservation for the long term. Projects within Biodiversity Hotspots have a strong focus on climate change, agriculture and biodiversity protection, indicating CWR conservation here could have a great positive impact on many sectors.

A comparison of global crop wild relative hotspots with theories on centres of plant domestication and diversity (Chapter 5)

Vavilov centres of diversity are widely regarded in the CWR community to be analogous with areas of high CWR diversity; however this has never been investigated for all CWR related to important crops for food security. To assess whether this claim was valid Chapter 5 examined four concepts on areas of crop domestication and diversity and assessed the congruence between concepts and CWR hotspots and distributions. Vavilov centres of diversity were found to have considerable overlap with CWR hotspots and CWR predictive distribution models, and were the most representative of the four concepts in terms of CWR. However, Vavilov centres of diversity are not totally equivalent to areas of high CWR diversity; CWR rich areas such as eastern USA, southeast Brazil, Europe and West Africa are not represented at all. Any CWR conservation strategies involving Vavilov centres should also strive to include these areas, to prevent genetic resources being overlooked and possibly eroded.

6.2 Limitations

The limitations that affected the work in this thesis included:

- A lack of quality, representative occurrence records for *in situ* gap analysis and production of robust SDMs. Particular focus is needed to collect more geo-referenced data on the 164 CWR with no occurrence records and the CWR which had fewer than 10 unique occurrences. Also there is a lack of occurrence data for some regions and countries worldwide giving an uneven view of CWR coverage. Areas such as China and Central Africa could be better represented by occurrence records if *ex situ* collecting efforts could be focussed there.

- Poor taxonomy of some crop gene pools and a lack of hybridisation data. The inventory could be greatly improved by revising the taxonomy of certain crop gene pools, such as citrus, mango and breadfruit and also by more hybridising experiments, particularly for less major crops, where breeding experiments have been somewhat neglected, as there is a paucity of literature covering this.

- Species distribution modelling. Predictive modelling is a useful technique, however, when occurrence datasets do not fully represent the native range of the individual taxon, bias can creep in. Biased occurrence datasets can lead to false assumptions in the modelling software therefore leading to overfitting in some cases and inaccurate predictions. Furthermore, SDMs generally use only environmental variables as inputs thus do not consider other important factors underlying a species distribution such as biotic interactions, evolutionary change or dispersal of species (Pearson and Dawson, 2003). Additionally, SDMs that have been projected into the future do not account for genetic adaptation or phenotypic plasticity.

- A lack of expert advice. Due to time constraints, it was not possible to involve CWR experts in the global *in situ* CWR conservation planning. This is a vital improvement that should be carried out to ensure the robustness of recommended future conservation strategies.

- Lack of genetic data. Genetic data was not available for the CWR occurrences modelled in the *in situ* gap analysis and reserve planning; instead, ELC maps were created per CWR to evaluate environmental niches as a proxy for genetic diversity. Although experiments involving ELC maps have been performed on lupins by Parra-Quijano *et al.* (2012b) to assess the validity of this approach, more experimentation is needed to discover whether this a suitable technique for determining genetic diversity for a wide range of CWR.

- Lack of realism in conservation planning. The conservation planning scenario was already sufficiently complex for an initial run, so layers such as threats and land costs were not incorporated. These should be incorporated in future work to increase the robustness of the selected sites for conservation.

- Drawing centres of crop domestication and diversity by hand in GIS software which could have introduced minor inconsistencies into the analysis.

6.3 Conclusion

Prevention of biodiversity loss and improving food security now and for the future are complex, multi-faceted objectives which require a holistic approach to resolve; as Alexander von Humbolt, the pioneer of environmentalism, said, “In this great chain of causes and effects, no single fact can be considered in isolation." Fully addressing these issues will require changes in agricultural systems, and perhaps more importantly, changes in social, economic and political systems and values to create a more sustainable Earth (Godfray *et al.*, 2010; Jarvis *et al.*, 2012; Erb *et al.*, 2016). Indeed, a step change is required when it comes to attitudes towards the environment and its protection; in Honduras alone, 109 indigenous rights and environmental activists have been murdered between 2010 and 2015 for protecting indigenous homelands from destructive industries such as mining, dams and agribusiness (Global Witness, 2016). Effective, long term conservation cannot be achieved without moving to a more respectful and sustainable approach towards the environment.

To improve food security worldwide from a CWR conservation perspective, there needs to be greater international cohesion, scientific advancement and greater long term funding for conservation of this priceless resource. The PGR conservation community needs to act decisively and quickly to conserve populations of CWR *in situ*, to ensure their long term availability to plant breeding, prevent genetic erosion and maintain persistence in natural habitats. The work presented in this thesis provides a key stepping stone to begin comprehensive conservation of priority CWR from a global perspective via the creation of the Harlan and de Wet CWR Inventory and the first systematic *in situ* gap analysis for over 1200 CWR related to crops which provide human food security. Practical implementation of a network of *in situ* CWR reserves is also explored through climate change analysis, genetic diversity analysis, reserve planning and investigating coincident areas of high biodiversity for complementary conservation.

The methodologies applied throughout this thesis are highly repeatable and will hopefully inspire other researchers to replicate these techniques at the local, national and regional levels for the improvement of *in situ* CWR conservation as a whole.

REFERENCES

Ahmad, F., Gaur, P.M. and Croser, J.S. (2005) Chickpea (Cicer arientinum L.). In: Singh, R., Jauhar, P. (eds.), *Volume 1 – Genetic Resources, Chromosome Engineering, and Crop Improvement: Grain Legumes*.CRC Press, Florida. Pp. 229–267.

Allnutt, T.F., McClanahan, T.R., Andréfouët, S., Baker, M., Lagabrielle, E., McClennen, C., Rakotomanjaka, A.J., Tianarisoa, T.F., Watson, R. and Kremen, C. (2012) Comparison of marine spatial planning methods in Madagascar demonstrates value of alternative approaches. *PloS ONE* 7(2): p.e28969.

Anderson, P. K., Cunningham, A. A., Patel, N. G., Morales, F. J., Epstein, P. R., and Daszak, P. (2004) Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* 19(10): 535–544.

Anderson, R. and Raza, A. (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus Nephelomys) in Venezuela. *Journal of Biogeography* 37: 1378–1393.

Ardron, J.A., Possingham, H.P. and Klein, C.J. (eds.) (2010) *Marxan Good Practices Handbook, Version 2*. Pacific Marine Analysis and Research Association, Victoria, BC, Canada. Pp. 165.

Arendt, A. A., Echelmeyer, K. A., Harrison, W. D., Lingle, C. S., and Valentine, V. B. (2002) Rapid wastage of Alaska glaciers and their contribution to rising sea level. *Science* 297(5580): 382–386.

Balmford, A., Green, J.M.H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M. and Manica, A. (2015) Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas. *PLoS Biology* 13(2): e1002074. doi:10.1371/journal.pbio.1002074.

Bauch, S.C., Birkenbach, A.M., Pattanayak, S.K. and Sills, E.O. (2015) Public health impacts of ecosystem change in the Brazilian Amazon. *Proceedings of the National Academy of Sciences* 112(24), 7414–7419.

Bebber, D.P., Ramotowski, M.A. and Gurr, S.J. (2013) Crop pests and pathogens move polewards in a warming world. *Nature Climate Change* 3(11): 985–988.

Berlingeri, C. and Crespo, M.B. (2012) Inventory of related wild species of priority crops in Venezuela. *Genetic Resources and Crop Evolution* 59(5): 655–681.

Bilz, M., Kell, S.P., Maxted, N. and Lansdown, R.V. (2011) *European Red List of Vascular Plants*. Publications Office of the European Union, Luxembourg.

Bothmer, von R., Jacobsen, N., Baden, C., Jørgensen, R.B. and Linde-Laursen, I. (1995) An ecogeographical study of the genus Hordeum. In: *Systematic and Ecogeographic Studies on Crop Genepools 7 Second edition*. International Plant Genetic Resources Institute, Rome.

Brar, D. (2005) Broadening the genepool and exploiting heterosis in cultivated rice. In: Toriyama K., Heong K.L. and Hardy B. (eds.), *Rice is life: scientific perspectives for the 21st Century*. Proceedings of the World Rice Research Conference, Tokyo and Tsukuba, Japan, 4–7 November 2004.

Brown, A.H.D. and Briggs, J.D. (1991) Sampling strategies for genetic variation in *ex situ* collections of endangered plant species. In: Falk, D.A and Holsinger, K.E. (eds.) *Genetics and Conservation of Rare Plants*. Oxford University Press, New York. Pp. 99–119.

Brown, A.H.D. and Marshall, D.R. (1995) A basic sampling strategy: theory and practice. In: Guarino, L., Ramanatha Rao, V. and Reid, R. (eds.), *Collecting Plant Genetic Diversity: Technical Guidelines*. Cambridge University Press, Cambridge. Pp. 75–91.

Brummitt, R.K. (2001) *World geographical scheme for recording plant distributions, Edition 2*. International Working Group on Taxonomic Databases for Plant Sciences. Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh.

Brummitt, N.A., Bachman, S.P., Griffiths-Lee, J., Lutz, M., Moat, J.F., Farjon, A., Donaldson, J.S., Hilton-Taylor, C., Meagher, T.R., Albuquerque, S. and Aletrari, E. (2015) Green plants in the red: a baseline global assessment for the IUCN Sampled Red List Index for Plants. *PloS ONE* 10(8): p.e0135152.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A. and Kinzig, A.P. (2012) Biodiversity loss and its impact on humanity. *Nature* 486(7401): 59–67.

Castañeda Álvarez, N.P., Vincent, H., Kell, S., Eastwood, R. and Maxted, N. (2011) Ecogeographic surveys. In: Guarino, L., Ramanatha Rao, V., Goldberg, E. (eds.) *Collecting plant genetic diversity: Technical guidelines. 2011 update*. Bioversity International, Rome. [online]Available at: http://cropgenebank.sgrp.cgiar.org/index.php?option=com_content&view=article&id=390&Itemid=557.

Castañeda-Álvarez, N.P., Khoury, C.K., Achicanoy, H.A., Bernau, V., Dempewolf, H., Eastwood, R.J., Guarino, L., Harker, R.H., Jarvis, A., Maxted, N., Müller, J.V., Ramirez-Villegas, J., Sosa, C.C., Struik,P.C., Vincent, H. andToll, J. (2016a) Global conservation priorities for crop wild relatives. *Nature Plants* 2, p.16022.

Castañeda-Álvarez, N.P., Khoury, C.K., Sosa, C.C., Sotelo, S., Vanegas, I., Calderón, S.S., Vincent, H., Harker, R.H., Bernau, V., Eastwood, R.J., Ramirez-Villegas, J., Dempewolf, H., Guarino, L., Toll, J., Jarvis, A., Müller, J., the Global Consortium of Crop Wild Relative Occurrence Data Providers and Maxted, N. (2016b) A Global Occurrence Dataset for Crop Wild Relatives. [online] Available at: http://www.cwrdiversity.org/checklist/cwr-occurrences.php.

CBD (2010a) *Global Strategy for Plant Conservation*. Secretariat of the Convention on Biological Diversity, Montreal.

CBD (2010b) *Conference of the Parties Decision X/2: Strategic plan for biodiversity 2011–2020*. Secretariat of the Convention on Biological Diversity, Montreal. [online] Available at: www.cbd.int/decision/cop/?id=12268 (Accessed 1 October 2014).

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. and Palmer, T.M. (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances* 1(5): e1400253. DOI: 10.1126/sciadv.1400253.

CEPF (2011) *Biodiversity hotspots ArcView shapefile and metadata*. [online] Available at: http://www.cepf.net/SiteAssets/CI_Biodiversity-Hotspots_2011_ArcView-Shapefile-and-Metadata.zip (Accessed 20 July 2013).

CEPF (2015) *2015 Annual Report*. The Critical Ecosystem Partnership Fund, Virginia, USA.

Challinor, A. J., Watson, J., Lobell, D. B., Howden, S. M., Smith, D. R. and Chhetri, N. (2014) A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change* 4: 287–291.

Challinor, A.J., Koehler, A.K., Ramirez-Villegas, J., Whitfield, S. and Das, B. (2016) Current warming will reduce yields unless maize breeding and seed systems adapt immediately. *Nature Climate Change*: doi:10.1038/nclimate3061.

Church, J. A., and White, N. J. (2006) A 20th century acceleration in global sea-level rise. *Geophysical Research Letters* 33(1).

Cobben, M.M.P., van Treuren, R., Castañeda-Álvarez, N.P., Khoury, C.K., Kik, C. and van Hintum, T.J.L. (2014) Robustness and accuracy of Maxent niche modelling for *Lactuca* species distributions in light of collecting expeditions. *Plant Genetic Resources: Characterization and Utilization* 1–9. doi: 10.1017/S1479262114000847.

Coleman-Jensen, A., Rabbitt, M., Gregory, C. and Singh, A. (2015) *Household Food Security in the United States in 2014*. Economic Research Report No. (ERR-194).

Conservation International (2016a) *Finding Nature's Voice, 2015 Annual Report*. [online] Available at: http://www.conservation.org/publications/documents/CI_FY15_AnnualReport.pdf (Accessed 09 June 2016).

Conservation International (2016b) *Impact Report 2015.* [online] Available at: http://www.conservation.org/publications/Documents/CI_2015ImpactReport.pdf (Accessed 09 June 2016).

Crop Wild Relatives Global Portal (2015) *Crop wild relatives in national inventories.* [online] Available at: http://www.cropwildrelatives.org/national-inventories/ (Accessed 15 January 2015).

Dalton, R. (2000) Biodiversity cash aimed at hotspots. *Nature* 406: 818.

D'Amen, M., Bombi, P., Pearman, P.B., Schmatz, D.R., Zimmermann, N.E. and Bologna, A. (2011) Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? *Biological Conservation* 144(3): 989–997.

Darwin, C. (1868) *The variation of animals and plants under domestication*. London, UK.

Davis, A.P., Gole, T.W., Baena, S. and Moat, J. (2012) The Impact of Climate Change on Indigenous Arabica Coffee (Coffea arabica): Predicting Future Trends and Identifying Priorities. *PLoS ONE* 7(11): e47981. doi:10.1371/journal.pone.0047981.

de Candolle, A. (1886) *Origins de Plantes Cultivées*. (English edition 1886). Paris, France.

DeFries, R., Hansen, A.J., Newton, A.C. and Hansen, M.C. (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications* 15: 19–26.

Dempewolf, H. Eastwood, R.J., Guarino, L., Khoury, C.K., Müller, J.V. and Toll, J. (2013) Adapting Agriculture to Climate Change : A Global Initiative to Collect, Conserve, and Use Crop Wild Relatives. *Agroecology and Sustainable Food Systems* 38: 369–377.

Deryng, D., Sacks, W.J., Barford, C.C. and Ramankutty, N. (2011) Simulating the effects of climate and agricultural management practices on global crop yield. *Global Biogeochemical Cycles* 25: GB2006, doi: http://dx.doi.org/10.1029/2009GB003765.

Diamond, J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature* 418: 700–707.

Dias, S., Dulloo, M.E. and Arnaud, E. (2012) The role of EURISCO in promoting use of agricultural biodiversity. In: Maxted, N., Dulloo, M.E., Ford-Lloyd, B.V., Frese, L., Iriondo, J.M. and Pinheiro de Carvalho, M.A.A. (eds.) *Agrobiodiversity Conservation: Securing the Diversity of Crop Wild Relatives and Landraces*. CAB International, Wallingford. Pp. 270─277.

Díaz, S., Fargione, J., Chapin, F.S. III and Tilman, D. (2006) Biodiversity Loss Threatens Human Well-Being. *PLoS Biology* 4(8): e277. doi:10.1371/journal.pbio.0040277.

Dudley, N. (ed.) (2008). *Guidelines for Applying Protected Area Management Categories*. IUCN, Gland, Switzerland.

Dulloo, M.E., Labokas, J., Iriondo, J.M., Maxted, N., Lane, A., Laguna, E., Jarvis, A. and Kell, S.P. (2008) Genetic reserve location and design. In: Iriondo, J.M., Maxted, N. and Dulloo, M.E. (eds.) *Conserving Plant Genetic Diversity in Protected Areas*. CAB International, Wallingford, UK. Pp. 23–64.

Duveiller, E., Singh, R.P. and Nicol, J.M. (2007) The challenges of maintaining wheat productivity: pests, diseases, and potential epidemics. *Euphytica* 157: 417–430.

ECPGR (2012) *Report of the 13th ECPGR Steering Committee Meeting.* Federal Ministry of Agriculture, Forestry, Environment and Water Management Austria on 4-7 December 2012. [online] Available at: http://www.ecpgr.cgiar.org/about-ecpgr/steering-committee/13th-sc-meeting/ (Accessed 6 March 2015).

Edwards, D. P., Sloan, S., Weng, L., Dirks, P., Sayer, J. and Laurance, W. F. (2014) Mining and the African Environment. *Conservation Letters* 7: 302–311. doi: 10.1111/conl.12076.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M. and E. Zimmermann, N. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151 doi: 10.1111/j.2006.0906-7590.04596.x.

Elith, J. and Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics* 40: 677–697.

Esquinas-Alcázar, J. (2005) Protecting crop genetic diversity for food security: political, ethical and technical challenges. *Nature Reviews Genetics* 6(12): 946─953.

European Environment Agency (2013) *Natura 2000 data - the European network of protected sites*. [online] Available at: http://www.eea.europa.eu/data-and-maps/data/natura-5 (Accessed 10 September 2014).

Evenson, R.E. and Gollin, D. (2001) *The Green Revolution at the End of the Twentieth Century*. Consultative Group on International Agricultural Research.

FAO (2001) *International Treaty on Plant Genetic Resources for Food and Agriculture*. Food and Agriculture Organization of the United Nations, Rome.

FAO (2008) *Climate Change and Biodiversity for Food and Agriculture*. Food and Agriculture Organization of the United Nations, Rome.

FAO (2010) *Second report on the State of the World's Plant Genetic Resources for Food and Agriculture*. Food and Agriculture Organization of the United Nations, Rome. [online] Availble at: http://www.fao.org/agriculture/seed/sow2/en/ (Accessed 25 July 2015).

FAO (2011a) *The Second Global Plan of Action for Plant Genetic Resources for Food and Agriculture*. Food and Agriculture Organization of the United Nations, Rome.

FAO (2011b) *World Agriculture Towards 2030/2050: The 2012 revision*. ESA E Working Paper No. 12-03. Food and Agriculture Organization of the United Nations, Rome. [online] Available at: http://www.fao.org/economic/esa/esag/en [Accessed 6 March 2015].

FAO (2011c) *Thirteenth Regular Session of the Commission on the Genetic Resources for Food and Agriculture*, CGRFA-13/11/Report. Food and Agriculture Organization of the United Nations, Rome. [online] Available at: http://www.fao.org/docrep/meeting/024/mc192e.pdf (Accessed 6 March 2015).

FAO (2012) *FAO Integrated Food Security Support Service*. Food and Agriculture Organization of the United Nations, Rome.

FAO (2013) *Towards the establishment of a global network for in situ conservation and on-farm management of PGRFA*. Report of Technical Workshop held in Rome, Italy 13th November, 2012. Food and Agriculture Organisation of the UN, Rome Italy. [online] Available at: http://www.fao.org/agriculture/crops/core-themes/theme/seedspgr/itwg/6th/technical-workshop/en/ (Accessed 5 April 2013).

FAO (2014) *Concept note on global networking on in situ conservation and on-farm management of plant genetic resources for food and agriculture*. Information document to the 7th Session of the Intergovernmental Working Group on Plant Genetic Resources for Food and Agriculture (CGRFA/WG-PGR-7/14/Inf.3, Commission for Genetic Resources for Food and Agriculture, Rome. [online] Available at: http://www.fao.org/3/a-ml477e.pdf (Accessed 6 March 2015).

FAO (2016) *Climate change and food security: risks and responses*. Food and Agriculture Organization of the United Nations, Rome.

FAO, IFAD and WFP (2013) *The State of Food Insecurity in the World 2013:The multiple dimensions of food security*. Food and Agriculture Organization of the United Nations, Rome.

FAO, IFAD and WFP (2015) *State of Food Insecurity in the World 2015. Meeting the 2015 international hunger targets: taking stock of uneven progress*. Food and Agriculture Organization of the United Nations, Rome.

FAOSTAT (2012) *FAOSTAT*. Food and Agriculture Organization of the United Nations, Rome. [online] Availbale at: http://faostat3.fao.org/home/index.html#HOME (Accessed 17 January 2012).

Feuillet, C., Langridge, P. and Waugh, R. (2008) Cereal breeding takes a walk on the wild side. *Trends in Genetics* 24: 24–32.

Fielder, H., Brotherton, P., Hosking, J., Hopkins, J.J., Ford-Lloyd, B. and Maxted, N. (2015) Enhancing the conservation of crop wild relatives in England. *PLoS ONE* 10: e0130804 doi: 10.1371/journal.pone.e0130804.

Finer, M., Jenkins, C.N., Pimm, S.L., Keane, B. and Ross, C. (2008) Oil and gas projects in the western Amazon: Threats to wilderness, biodiversity, and indigenous peoples. *PLoS ONE* 3: 1─9.

Fitter, R. and Fitter, M. (1987) *The Road to Extinction*. International Union for Conservation of Nature, Gland, Switzerland.

Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L., and Gurr, S. J. (2012) Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484(7393): 186–194.

Foley, J.A., Asner, G.P., Costa, M.H., Coe, M.T., DeFries, R., Gibbs, H.K., Howard, E.A., Olson, S., Patz, J. and Ramankutty, N. (2007) Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment* 5: 25─32.

Ford-Lloyd, B. and Maxted, N. (1993) Preserving diversity. *Nature* 361: 579.

Ford-Lloyd, B.V., Maxted, N. and Kell, S.P. (2008) Establishing conservation priorities for crop wild relatives. In: Maxted, N., Ford-Lloyd, B.V., Kell, S.P., Iriondo, J.M., Dulloo, M.E. and Turok, J. (eds.), *Crop Wild Relative Conservation and Use*. CABI Publishing, Wallingford. Pp. 110–119.

Ford-Lloyd, B.V., Schmidt, M., Armstrong, S.J., Barazani, O., Engels, J., Hadas, R., Hammer, K., Kell, S.P., Kang, D.M., Khoshbakht, K., Li, Y., Long, C., Lu, B-R., Ma, K., Nguyen, V.T., Qiu, L., Ge, S., Wei, W., Zhang, Z. and Maxted, N. (2011) Crop Wild Relatives – Undervalued, Underutilized and under Threat? *BioScience* 61: 559–565.

Ford-Lloyd, B., Engels, J.M.M. and Jackson, M. (2014) Genetic resources and conservation challenges under the threat of climate change. In: Jackson, M., Ford-Lloyd, B. and Parry, M. (eds.), *Plant Genetic Resources and Climate Change*. CABI Publishing, Wallingford. Pp. 16–37.

Gabrielian, E. and Zohary, D. (2004) Wild relatives of food crops native to Armenia and Nakhichevan. *Flora Mediterranea* 14: 5–80.

Gadgil, M., Niwas Singh, S., Nagendra, H. and Chandran, M.D.S. (1996) *In situ conservation of wild relatives of cultivated plants: guiding principles and a case study*. Food and Agriculture Organization of the United Nations, Rome.

Gaston, K. J. (2000) Global patterns in biodiversity. *Nature* 405 (6783): 220–227. doi:10.1038/35012228.

GBIF (2013) *Biodiversity occurrence data*. [online] Available at: http://data.gbif.org (Accessed 10 March 2013).

GCDT (2011) *$50 million pledge for climate change adaptation*. Global Crop Diversity Trust, Rome.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. and Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology* 11: 97–105.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M. and Burgess, N.D. (2013) Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation* 161: 230–238.

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., Robinson, S., Thomas, S. M. and Toulmin, C. (2010) Food security: the challenge of feeding 9 billion people. *Science* 327(5967): 812–818.

GRIN (2015) *Germplasm Resources Information Network – (GRIN).* USDA, ARS, National Genetic Resources Program. National Germplasm Resources Laboratory, Beltsville, Maryland. [online] Available at: http://www.ars-grin.gov.4/cgi-bin/npgs/html/tax_search.pl?language=en (Accessed 29 January 2015).

GRIN Global (2015) *U.S. National Plant Germplasm System: Query Crop Relatives in GRIN.* [online] Available at: https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearchcwr.aspx (Accessed 10 December 2015).

Groombridge, B. and Jenkins, M.D. (2002) *World Atlas of Biodiversity*. University of California Press, Berkeley.

Groves, C.R. (2003) *Drafting a conservation blueprint: a practitioner's guide to planning for biodiversity*. Island Press, Washington, USA.

Guarino, L. and Lobell, D.B. (2011) A walk on the wild side. *Nature Climate Change* 1: 374–375.

Gur, A. and Zamir, D. (2004). Unused natural variation can lift yield barriers in plant breeding. *PLoS Biology* 2:e245.

Hajjar, R. and Hodgkin, T. (2007) The use of wild relatives in crop improvement: A survey of developments over the last 20 years. *Euphytica* 156: 1–13.

Hanelt, P., Institute of Plant Genetics and Crop Plant Research (2001) *Mansfeld's encyclopedia of agricultural and horticultural crops*. Springer, Berlin.

Harlan, J. (1971) Agricultural origins, centers and noncenters. *Science* 174: 468–474.

Harlan, J. R. (1992) *Crops and man, second edition.* American Society of Agronomy, Madison.

Harlan, J.R. and de Wet, J.M.J. (1971) Towards a rational classification of cultivated plants. *Taxon* 20: 509–517.

Hawkes, J. G., Maxted, N. and Ford-Lloyd, B. V. (2000) *The ex situ conservation of plant genetic resources*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hein, L. and Gatzweiler, F. (2006) The economic value of coffee (Coffea arabica) genetic resources. *Ecological Economics* 60 (1): 176–185.

Hengl, T., de Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J.G., Walsh, M.G. and Gonzalez, M.R. (2014) SoilGrids1km—global soil information based on automated mapping. *PLoS ONE* 9(8): p.e105992.

Henry, R.J. (2014) Genomics strategies for germplasm characterization and the development of climate resilient crops. *Frontiers in Plant Science* 5: 68.

Heywood, V.H. and Dulloo, M.E. (2005) *In situ conservation of wild plant species – a critical global review of good practices*. International Plant Genetic Resources Institute, Rome.

Hijmans, R.J., Cruz, M., Rojas, E. and Guarino, L. (2001) *DIVA-GIS Manual. Version 1.4. A geographic information system for the management and analysis of genetic resources data*. International Potato Center, (CIP), Lima, Peru.

Hijmans, R.J., Guarino, L., Cruz,M., and Rojas, E.(2001) Computer tools for spatial analysis of plant genetic resources data: 1.DIVA-GIS. *Plant Genetics Resources Newsletter* 127, 15–19.

Hijmans, R.J., Cameron, S.E., Para, J.L., Jones, P.G. and Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 965–1978.

Hijmans, R.J., Guarino, L., Jarvis, A., O'Brien, R., Mathur, P., Bussink, C., Cruz, M., Barrantes, I., and Rojas, E. (2005*) DIVA-GIS. Version 5.2. Manual*. [online] Available ar: http://www.divasgis.org (Accessed 1 March 2011).

Hoegh-Guldberg, O., and Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science* 328(5985): 1523–1528.

Hoekstra, J.M., Molnar, J.L, Jennings, M., Revenga, C., Spalding, M.D., Boucher, T.M., Robertson, J.C., Heibel, T.C. and Ellison, K. (2010) *The Atlas of Global Conservation: Changes, Challenges, and Opportunities to Make a Difference.* University of California Press, California.

Hoisington, D., Khairallah, M., Reeves, T., Ribaut , J.-M., Skovmand, B., Taba, S. and Warburton, M.(1999) Plant genetic resources: What can they contribute toward increased crop productivity? *PNAS* 96: 5937–5943.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. and O'Connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* dx.doi.org/10.1038/nature11118.

Hoyt, E. (1988) *Conserving the Wild Relatives of Crops*. IBPGR, IUCN, WWF, Rome and Gland.

Hummer, K. and Hancock, J. (2015) Vavilovian centers of plant diversity: Implications and impacts. *HortScience* 50:780–783.

Hunter, D. and Heywood, V.H. (eds.) (2011) *Crop Wild Relatives: A Manual of In situ Conservation*. Earthscan, London.

Idohou, R., Assogbadjo, A.E., Fandohan, B., Gouwakinnou, G.N., Glèlè Kakaï, R.L., Sinsin, B. and Maxted, N. (2013) National inventory and prioritization of the crop wild relatives: case study for Benin. *Genetic Resources and Crop Evolution* 60: 1337–1352.

ILDIS (2011) LegumeWeb. International Legume Database and Information Service. [online] Available at: http://www.ildis.org/cgi-bin/Araneus.pl (Accessed 1 April 2011).

IPCC (2007) *Fourth Assessment Report Climate Change 2007: Synthesis Report.* Intergovernmental Panel on Climate Change, Geneva, Switzerland.

IPCC (2014) *Climate Change 2014: Synthesis report: Longer report*. [online] Available at: http://www.ipcc.ch/pdf/assessment-report/ar5/syr/SYR_AR5_LONGERREPORT.pdf (Accessed 3 November 2014).

Iriondo, J.M., Maxted, N. and Dulloo, M.E. (eds.) (2008) *Conserving Plant Genetic Diversity in Protected Areas*. CAB International, Wallingford, U.K.

Iriondo, J. M., Maxted, N., Kell, S. P., Ford-lloyd, B. V., Lara-Romero, C., Labokas, J. and Magos Brehm, J. (2012) Quality standards for genetic reserve conservation of crop wild relatives. In: N. Maxted, M. E. Dulloo, B. V. Ford-Lloyd, L. Frese, J. Iriondo and M. A. A. Pinheiro de Carvalho (eds.), *Agrobiodiversity conservation: securing the diversity of crop wild relatives and landraces*. CABI, Wallingford. Pp. 72–77.

IUCN (2015) 2015 *IUCN Red List of Threatened Species*. [online] Available at: www.iucnredlist.org (Accessed 21 July 2015).

IUCN and UNEP-WCMC (2012) *The World Database on Protected Areas (WDPA).* UNEP-WCMC, Cambridge, UK. [online] Available at: www.protectedplanet.net (Accessed 12 December 2012).

Jain, H.K. and Kharkwal, M.C. (eds.) (2012) *Plant breeding: Mendelian to molecular approaches*. Springer Science & Business Media.

Jarvis, A., Williams, K., Williams, D., Guarino, L., Caballero, P.J. and Mottram, G. (2005) Use of GIS for optimizing a collecting mission for a rare wild pepper (Capsicum flexuosum Sendtn.) in Paraguay. *Genetic Resources and Crop Evolution* 52: 671–682.

Jarvis, A., Lane, A. and Hijmans, R.J. (2008) The effect of climate change on crop wild relatives. Agriculture, Ecosystems and Environment 126: 13–23.

JiUng, J., YeonGyu, K., Jena, K.K., YoungChan, C., JeomHo, L., MyeongKi, K., HaCheol, H., JongHee, L., JeongJu, K., ImSoo, C. and EungGi, J. (2014) A brown planthopper resistant and high grain quality rice variety 'Anmi' developed by molecular breeding method. *Korean Journal of Breeding Science*, 46(2): 152–159.

Jonas, H.D, Barbuta, V., Jonas, H.C, Kothari, A.and Nelson, F. (2014) New Steps of Change: Looking Beyond Protected Areas to Consider Other Effective Area-Based Conservation Measures. *Parks* 20(2): 111–128.

Jones, P.D., Lister, D.H., Jaggard, K.W. and Pidgeon, J.D. (2003) Future climate change impact on the productivity of sugar beet (Beta vulgaris L.) in Europe. *Climatic Change* 58: 93–108.

Jones, J.D., Witek, K., Verweij, W., Jupe, F., Cooke, D., Dorling, S., Tomlinson, L., Smoker, M., Perkins, S. and Foster, S. (2014) Elevating crop disease resistance with cloned genes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 369(1639): p.20130087.

Joppa, L.N. and Pfaff, A. (2009) High and far: biases in the location of protected areas. *PLoS ONE* 4(12) :e8273.

Joppa, L.N., Loarie, S.R. and Pimm, S.L. (2008) On the protection of protected areas. *PNAS* 105: 6673–6678.

Jordan, J., Butler, D., Henzell, B., Drenth, J. and McIntyre, L. (2004) *Diversification of Australian sorghum using wild relatives, new directions for a diverse planet*. Proceedings of the 4th International Crop Science Congress, Brisbane, Australia, 26 September–1 October 2004.

Juffe-Bignoli, D., Burgess, N.D., Bingham, H., Belle, E.M.S., de Lima, M.G., Deguignet, M., Bertzky, B., Milam, A.N., Martinez-Lopez, J., Lewis, E., Eassom, A., Wicander, S., Geldmann, J., van Soesbergen, A., Arnell, A.P., O'Connor, B., Park, S., Shi, Y.N., Danks, F.S., MacSharry, B. and Kingston, N. (2014) *Protected Planet report 2014*. UNEP-WCMC, Cambridge, UK.

Kantar, M.B., Sosa, C.C., Khoury, C.K., Castañeda-Álvarez, N.P., Achicanoy, H.A., Bernau, V., Kane, N.C., Marek, L., Seiler, G. and Rieseberg, L.H. (2015) Ecogeography and utility to plant breeding of the crop wild relatives of sunflower (Helianthus annuus L.). *Frontiers in Plant Science* 6:841. doi: 10.3389/fpls.2015.00841.

Kareiva, P. and Marvier, M. (2003) Conserving Biodiversity Coldspots recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. *American Scientist* 91(4): 344–351.

Kastner, T., Rivas, M.J.I., Koch, W. and Nonhebel, S. (2012) Global changes in diets and the consequences for land requirements for food. *PNAS* 109: 6868–6872.

Kell SP, Knüpffer H, Jury SL, Ford-Lloyd BV and Maxted N (2008) Crops and wild relatives of the Euro-Mediterranean region: making and using a conservation catalogue. In: Maxted N, Ford-Lloyd BV, Kell SP, Iriondo J, Dulloo E and Turok J (eds.) *Crop Wild Relative Conservation and Use*. CABI Publishing, Wallingford. Pp. 69–109.

Kell, S.P., Maxted, N., and Bilz, M. (2012) European crop wild relative threat assessment: knowledge gained and lessons learnt. In: Maxted, N., Dulloo, M.E., Ford-Lloyd, B.V., Frese, L.L., Iriondo, J.M. and Pinheiro de Carvalho, M.A.A. (eds.), *Agrobiodiversity Conservation: Securing the Diversity of Crop Wild Relatives and Landraces*. CAB International, Wallingford. Pp. 218–242.

Kell, S., Qin, H., Chen, B., Ford-Lloyd, B., Wei, W. and Maxted, N. (2015) China's crop wild relatives: Diversity for agriculture and food security. *Agriculture, Ecosystems and Environment*, doi:10.1016/j.agee.2015.02.012.

Kelley, C.P., Mohtadi, S., Cane, M.A., Seager, R. and Kushnir, Y. (2015) Climate change in the Fertile Crescent and implications of the recent Syrian drought. *PNAS* 112 (11): 3241‒3246.

Khoury, C.K., Greene, S., Wiersema, J., Maxted, N., Jarvis, A. and Struik, P.C. (2013) An Inventory of Crop Wild Relatives of the United States. *Crop Science* http://dx.doi.org/10.2135/cropsci2012.10.0585.

Khoury, C.K., Bjorkman, A.D., Dempewolf, H., Ramirez-Villegas, J., Guarino, L., Jarvis, A., Rieseberg, L.H. and Struik, P.C. (2014) Increasing homogeneity in global food supplies and the implications for food security. *PNAS* 111(11): 4001–4006.

Laurance, W.F., Useche, D.C., Rendeiro, J., Kalka, M., Bradshaw, C.J., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P. and Arroyo-Rodriguez, V. (2012) Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489(7415): 290–294.

Lessmann, J., Munoz, J. and Bonaccorso, E. (2014) Maximizing species conservation in continental Ecuador: a case of systematic conservation planning for biodiverse regions. *Ecology and Evolution* 4(12): .2410–2422.

Leverington, F., Costa, K.L., Pavese, H., Lisle, A. and Hockings, M. (2010) A global analysis of protected area management effectiveness. *Environmental Management,* 46(5): 685–698.

Li, X., Takahashi, T., Suzuki, N. and Kaiser, H.M. (2011) The impact of climate change on maize yields in the United States and China. *Agricultural Systems* 104: 348–353.

Lira, R., Téllez, O. and Dávila, P. (2009) The effects of climate change on the geographic distribution of Mexican wild relatives of domesticated Cucurbitaceae. *Genetic Resources and Crop Evolution* 56: 691–703.

Lobell, D.B., Burke, M.B., Tebaldi, C., Mastrandrea, M.D., Falcon, W.P. and Naylor, R.L. (2008) Prioritizing climate change adaptation needs for food security in 2030. *Science* 319: 607–610.

Lobell, D.B., M. Bänziger, C. Magorokosho, and Vivek, B. (2011) Nonlinear heat effectson African maize as evidenced by historical yield trials. *Nature Climate Change* 1: 42–45.

Luck, J., Spackman, M., Freeman, A., Trebicki, P., Griffiths, W., Finlay, K. and Chakraborty, S. (2011) Climate change and diseases of food crops. *Plant Pathology* 60: 113–121.

Mace, G.M., Balmford, A., Boitani, L., Cowlishaw, G., Dobson, A.P., Faith, D.P., Gaston, K.J., Humphries, C.J., Vane-Wright, R.I., Williams, P.H. and Lawton, J.H. (2000) It's time to work together and stop duplicating conservation efforts…. *Nature* 405(6785): 393–393.

Mace, G.M., Hails, R.S., Cryle, P., Harlow, J. and Clarke, S.J. (2015) Towards a risk register for natural capital. Journal of Applied Ecology 27: 641–653.

MacKinnon, K. (2016) Sound Investments. In: L. N. Joppa, J. E. M. Baillie and Robinson, J.G. (eds.) *Protected Areas: Are They Safeguarding Biodiversity?* John Wiley & Sons, Ltd, Chichester, UK. Pp. 49–65.

Magos Brehm, J., Maxted, N., Ford-Lloyd, B.V. and Martins-Loução, M.A. (2008) National inventories of crop wild relatives and wild harvested plants: case-study for Portugal. *Genetic Resources and Crop Evolution* 55: 779–796.

Magos Brehm, J., Maxted, N., Martins-Loução, M.A. and Ford-Lloyd, B.V. (2010) New approaches for establishing conservation priorities for socio-economically important plant species. *Biodiversity Conservation* 19: 2715–2740.

Marchese, C. (2015) Biodiversity hotspots: A shortcut for a more complicated concept. *Global Ecology and Conservation* 3: 297–309.

Marfil, C.F., Hidalgo, V. and Masuelli, R.W. (2015) *In situ* conservation of wild potato germplasm in Argentina: example and possibilities. *Global Ecology and Conservation* 3: 461–476.

Mascia, M.B. and Pailler, S. (2011) Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. *Conservation letters* 4(1): 9–20.

Maseyk, F.J., Mackay, A.D., Possingham, H.P., Dominati, E.J. and Buckley, Y.M. (2016) Managing Natural Capital Stocks for the Provision of Ecosystem Services. *Conservation Letters* doi: 10.1111/conl.12242.

Maxted, N., Ford-Lloyd, B.V. and Hawkes, J.G. (1997a) *Plant genetic conservation: the in situ approach.* Chapman & Hall, London.

Maxted, N., Hawkes, J.G., Guarino, L. and Sawkins, M. (1997b) The selection of taxa for plant genetic conservation. *Genetic Resources and Crop Evolution* 44: 337–348.

Maxted, N., Ford-Lloyd, B.V. and Hawkes, J.G. (1997c) Complementary conservation strategies. In: Maxted, N., Ford-Lloyd, B.V. and Hawkes, J.G. (eds.), *Plant Genetic Conservation: The In situ Approach*. Chapman & Hall, London. Pp. 20–55.

Maxted, N. and Ambrose, M. (2001) Peas (Pisum L.). In: Maxted, N. and Bennett, S.J. (eds.), *Plant Genetic Resources of Legumes in the Mediterranean*. Kluwer Academic Publishers, The Netherlands.

Maxted, N. (2003) Conserving the genetic resources of crop wild relatives in European protected areas. *Biological Conservation* 113: 411–417.

Maxted, N., Ford-Lloyd, B.V., Jury, S.L., Kell, S.P. and Scholten, M.A. (2006) Towards a definition of a crop wild relative. *Biodiversity Conservation* 15: 2673–2685.

Maxted, N., Iriondo, J.M., Dulloo, M.E. and Lane, A. (2008a) Introduction: The integration of PGR conservation with protected area management. In: Iriondo, J.M., Maxted, N. and Dulloo, M.E. (eds.), *Conserving plant genetic diversity in protected areas*. CABI Publishing, Wallingford. Pp. 1–22.

Maxted, N., Dulloo, E., Ford-Lloyd, B., Iriondo, J. and Jarvis, A. (2008b) Gap analysis: a tool for complementary genetic conservation assessment. *Diversity and Distributions* 14: 1018–1030.

Maxted, N., Iriondo, J., De Hond, L., Dulloo, E., Lefèvre, F., Asdal, A. Kell, S.P. and Guarino, L. (2008c) Genetic Reserve Management. In: Iriondo, J.M., Maxted, N. and Dulloo, E. (eds.), *Plant Genetic Population Management*. CAB International, Wallingford. Pp. 65–87.

Maxted, N. and Kell, S. (2009) *Establishment of a global network for the in situ conservation of Crop Wild Relatives: status and needs.* Background Study Paper No. 39. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome.

Maxted, N., Castañeda Álvarez, N.P., Vincent, H. and Magos Brehm, J. (2011a) Chapter 41: Gap analysis: A tool for genetic conservation. In: Guarino, L., Ramanatha Rao, V. and Goldberg, E. (eds.) *Collecting Plant Genetic Diversity: Technical Guidelines - 2011 Update*. Bioversity International, Rome, Italy.

Maxted, N., Dulloo, M.E., Ford-Lloyd, B.V., Frese, L., Iriondo, J.M. and Pinheiro de Carvalho, M.A.A. (eds.) (2011b) *Agrobiodiversity Conservation: Securing the Diversity of Crop Wild Relatives and Landraces*. CAB International, Wallingford.

Maxted, N., Hargreaves, S., Kell, S.P., Amri, A., Street, K., Shehadeh, A., Piggin, J. and Konopka, J. (2012a) Temperate forage and pulse legume genetic gap analysis. *Bocconea* 24: 5–36.

Maxted, N., Kell, S.P., Ford-Lloyd, B.V., Dulloo, M.E. and Toledo, A. (2012b) Toward the systematic conservation of global crop wild relative diversity. *Crop Science* 52: 774–785.

Maxted, N. (2015) Comment in: Goldenberg, S. *The doomsday vault: the seeds that could save a post-apocalyptic world*. The Guardian. [online] Available at: http://www.theguardian.com/science/2015/may/20/the-doomsday-vault-seeds-save-postapocalyptic-world.

Maxted, N., Amri, A., Castañeda- Álvarez, N.P., Dias, S., Dulloo, M.E., Fielder, H., Ford-Lloyd, B.V., Iriondo, J.M., Magos Brehm , J., Nilsen, L.B., Thormann, I., Vincent, H. and Kell, S.P. (2016) Joining up the dots: a systematic perspective of crop wild relative conservation and use. In: Maxted, N., Ehsan Dulloo, M. and Ford-Lloyd, B.V. (eds.) *Enhancing Crop Genepool Use: Capturing Wild Relative and Landrace Diversity for Crop Improvement.* CAB International, Wallingford, UK. ISBN-13: 978-1-78064-613-8.

McCallum, ML. (2015) Vertebrate biodiversity losses point to a sixth mass extinction. *Biodiversity and Conservation*. DOI 10.1007/s10531-015-0940-6.

McCarthy, D.P., Donald, P.F., Scharlemann, J.P., Buchanan, G.M., Balmford, A., Green, J.M., Bennun, L.A., Burgess, N.D., Fishpool, L.D., Garnett, S.T., Leonard, D.L., Maloney, R.L., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D.A. and Butchart, S.H. (2012) Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. *Science* 338(6109): 946–949.

McCouch, S., Baute, G. J., Bradeen, J., Bramel, P., Bretting, P. K., Buckler, E., Burke, J. M., Charest, D., Cloutier, S., Cole, G., Dempewolf, H., Dingkuhn, M., Feuillet, C., Gepts, P., Grattapaglia, D., Guarino, L., Jackson, S., Knapp, S., Langridge, P., Lawton-Rauh, A., Lijua, Q., Lusty, C., Michael, T., Myles, S., Naito, K., Nelson, R. L., Pontarollo, R., Richards, C. M., Rieseberg, L., Ross-Ibarra, J., Rounsley, S., Hamilton, R. S., Schurr, U., Stein, N., Tomooka, N., van der Knaap, E., van Tassel, D., Toll, J., Valls, J., Varshney, R. K., Ward, J., Waugh, R.,Wenzl, P. and Zamir, D. (2013) Feeding the future. *Nature* 499: 23–24.

Merow, C., Smith, M.J. and Silander, J.A. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecogeography* 36(10): 1058–1069.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis.* Island Press, Washington, DC.

Mittermeier, R.A., Myers, N., Thomsen, J.B., Da Fonseca, G.A. and Olivieri, S. (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12(3): 516–520.

Mittermeier, R.A., Robles, G.P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. and Da Fonseca, G.A.B. (2004) *Hotspots revisited*. CEMEX, Mexico.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M. and Gascon, C. (2011) Global biodiversity conservation: the critical role of hotspots. In: Zachos, F.E. and Habel, J.C. (eds.), *Biodiversity Hotspots*. Springer Publishers, London. Pp. 3–22.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. and Worm, B. (2011) How Many Species Are There on Earth and in the Ocean? *PLoS Biology* 9(8): e1001127. doi:10.1371/journal.pbio.1001127.

Moray, C., Game, E.T. and Maxted, N. (2014) Prioritising *in situ* conservation of crop resources: A case study of African cowpea (Vigna unguiculata). *Nature Scientific reports* 4.

Muehlbauer, F. and McPhee, K.E. (2005) Lentil (Lens culinaris Medik.). In: Singh, R., and Jauhar, P. (eds.), *Volume 1– Genetic Resources, Chromosome Engineering, and Crop Improvement: Grain Legumes*.CRC Press, Florida. Pp. 268–280.

Myers, N. (1988) Threatened biotas: "Hot spots" in tropical forests. *The Environmentalist* 8: 1–20.

Myers, N. (1990) The biodiversity challenge: Expanded hot spots analysis. *The Environmentalist* 10: 243–256.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Myers, N. (2003) Biodiversity hotspots revisited. *BioScience* 53(10): 916–917.

Naimi, B. (2015) USDM: Uncertainty Analysis for Species Distribution Models. R package version 1.1-15. [online] Available at: https://cran.r-project.org/web/packages/usdm/.

Nassar, N.M.A. (2003) Gene flow between cassava, Manihot esculenta Crantz, and wild relatives. *Genetics and Molecular Research* 2(4): 334–347.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S. and Stattersfield, A.J. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436(7053): 1016–1019.

Palm, C.A., Smuklera, S.M., Sullivana, C.C., Mutuoa, P.K., Nyadzia, G.I. and Walsh, M.G. (2010) Identifying potential synergies and trade-offs for meeting food security and climate change objectives in sub-Saharan Africa. *PNAS* 107: 19661–19666.

Panella, L. and Lewellen, R.T. (2007) Broadening the genetic base of sugar beet: introgression from wild relatives. *Euphytica* 154: 383–400.

Parra-Quijano, M., Draper, D. and Iriondo, J.M. (2007) GIS-based evaluation of the *in situ* conservation of a crop wild relative: the case of Spanish lupins. *Bocconea* 21: 105–116.

Parra-Quijano, M., Iriondo, J.M. and Torres, E. (2012a) Ecogeographical land characterization maps as a tool for assessing plant adaptation and their implications in agrobiodiversity studies. *Genetic Resources and Crop Evolution* 59: 205–217.

Parra-Quijano, M., Iriondo, J.M., and Torres, E. (2012b). Improving representativeness of genebank collections through species distribution models, gap analysis and ecogeographical maps. *Biodiversity and Conservation* 21: 79–96.

Parra-Quijano, M., Torres, E., Iriondo, J.M. and López, F. (2014*) CAPFITOGEN Tools User Manual Version 1.2.* International Treaty on Plant Genetic Resources for Food and Agriculture, FAO, Rome.

Parfitt, J., Barthel, M. and Macnaughton, S. (2010) Food waste within food supply chains: quantification and potential for change to 2050. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365(1554): 3065–3081.

Pearson, R.G. and Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12(5): 361–371.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Pickering, R., Steffenson, B.J., Hill, A.M. and Borovkova I. (1998) Association of leaf rust and powdery mildew resistance in a recombinant derived from a Hordeum vulgare x H. bulbosum hybrid. *Plant Breeding* 117: 83–84.

Pimentel, D., Wilson, C., McCullum, C., Huang, R., Owen, P., Flack, J., Tran, Q., Saltman, T. and Cliff, B. (1997) Economic and environmental benefits of biodiversity. *BioScience* 47: 747–757.

Pimm S.L., Russell G.J., Gittleman J.L. and Brooks T.M. (1995) The future of biodiversity. *Science* 269: 347.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. and Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344(6187): 1246752.

Porter, J.R., Xie, L., Challinor, A.J., Cochrane, K., Howden, S.M., Iqbal, M.M., Lobell, D.B. and Travasso, M.I. (2014). Food security and food production systems. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R. and White, L.L. (eds.), *Climate Change 2014: Impacts, Adaptation and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. Pp. 485-533.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., and Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution* 25: 345─353.

Prescott-Allen, R. and Prescott-Allen, C. (1988) *Genes From the Wild: Using Wild Genetic Resources for Food and Raw Materials Second edition*. International Institute for Environment and Development/Earthscan Publications, London.

PwC (2013) *Crop wild relatives: A valuable resource for crop development*. Price Waterhouse Cooper. [online] Available at: http://pwc.blogs.com/files/pwc-seed-bank-analysis-for-msb-0713.pdf.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. [online] Available at: http://www.R-project.org/.

Ramirez-Villegas, J., Khoury, C., Jarvis, A., Debouck, D.G., and Guarino, L. (2010) A gap analysis methodology for collecting crop genepools: a case study with Phaseolus beans. *PLoS ONE* 5(10): e13497. doi:10.1371/journal.pone.0013497.

Ramsar (2016) Ramsar Sites Information Service: Deltas del Estero Real y Llanos de Apacunca. [online] Available at: https://rsis.ramsar.org/ris/1136?language=en (Accessed 4 June 2016).

Rebelo, A.G. and Siegfried, W.R. (1990) Protection of Fynbos vegetation: Ideal and real-world options. *Biological Conservation* 54(1): 15–31.

Rebelo, A.G. and Siegfried, W.R. (1992) Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. *Conservation Biology* 6(2): 243–252.

Rebelo, A.G. (1994). Iterative selection procedures: centres of endemism and optimal placement of reserves. *Strelitzia* 1: 231–257.

Redden, R. (2015) Wild relatives for the crop improvement challenges of climate change: the adaptation range of crops. In: Redden, R., Yadav, S.S., Maxted, N., Dulloo, M.E., Guarino, L. and Smith, P. (eds.), *Crop Wild Relatives and Climate Change*. John Wiley & Sons, New Jersey, USA. Pp. 61–76.

Reif, J.C., Zhang, P., Dreisigacker, S., Warburton, M.L., van Ginkel, M., Hoisington, D., Bohn, M. and Melchinger, A.E. (2005). Wheat genetic diversity trends during domestication and breeding. *Theoretical and Applied Genetics* 110(5): 859–864.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Royal Botanic Gardens Kew (2008) Seed Information Database (SID). Version 7.1. [online] Available at: http://data.kew.org/sid/ (Accessed 1 January 2011).

Royal Botanic Gardens Kew (2011) The Plant List. [online] Available at: http://www.theplantlist.org/ (Accessed 1 April 2011).

Rubenstein, K.D., Heisey, P., Shoemaker, R., Sullivan, J. and Frisvold, G. (2005) *Crop Genetic Resources: An Economic Appraisal, Economic Information Bulletin No. (EIB2.* United States Department of Agriculture. Pp. 47.

Rubio Teso, M.L., Iriondo, J.M., Parra, M. and Torres, E. (2013) National strategy for the conservation of crop wild relatives of Spain. PGR Secure. [online] Available at: http://www.pgrsecure.bham.ac.uk/sites/default/files/documents/public/National_CWR_Conservation_Strategy_Spain.pdf .

Safriel, U.N., Anikster, Y. and Waldman, M. (1997) Management of nature reserves for conservation of wild relatives and the significant of marginal populations. *Bocconea* 7: 233–239.

Schmidhuber, J. andTubiello, F.N. (2007) Global food security under climate change. *PNAS* 104: 19703–19708.

Sebolt, A.M., Shoemaker, R.C. and Diers, B.W. (2000) Analysis of a quantitative trait locus allele from wild soybean that increases seed protein concentration in soybean. *Crop Science* 40: 1438–1444.

Sharma, H.C. and Gill, B.S. (1983) Current status of wide hybridization in wheat. *Euphytica* 32: 17–31.

Shehadeh, A., Amri, A. and Maxted, N. (2013) Ecogeographic survey and gap analysis of Lathyrus L. species. *Genetic Resources and Crop Evolution* doi: http://dx.doi.org/10.1007/s10722-013-9977-0.

Smith, R.J, Muir, R.D, Walpole, M.J., Balmford, A.and Leader-Williams, N. (2003) Governance and the loss of biodiversity. *Nature* 426: 67–70.

Stocker, T.F., Qin, D., Plattner, G.-K., Alexander, L.V., Allen, S.K., Bindoff, N.L., Bréon, F.-M., Church, J.A., Cubasch, U., Emori, S., Forster, P., Friedlingstein, P., Gillett, N.,Gregory, J.M., Hartmann, D.L., Jansen, E., Kirtman, B., Knutti, R., Krishna Kumar, K.,Lemke, P., Marotzke, J., Masson-Delmotte, V., Meehl, G.A., Mokhov, I.I., Piao, S., Ramaswamy, V., Randall, D., Rhein, M., Rojas, M., Sabine, C., Shindell, D., Talley, L.D., Vaughan, D.G. and Xie, S.-P. (2013) Technical Summary. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P.M. (eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Stolton, S., Maxted, N., Ford-Lloyd, B., Kell, S.P. and Dudley, N. (2006). *Food Stores: Using Protected Areas to Secure Crop Genetic Diversity*. WWF Arguments for protection series. WWF, Gland, Switzerland.

Stolten, S., Maxted, N., Ford-Lloyd, B., Kell, S. and Dudley, N. (2010) *Food stores: protected areas conserving crop wild relatives and securing future food stocks*. Arguments for Protected Areas: Multiple Benefits for Conservation and Use. Earthscan, London and Washington DC. Pp.53–69.

Suszkiw, J. (2005) Hessian Fly-Resistant Wheat Germplasm Available. Agricultural Research Service, News and Events, United States Department of Agriculture.

Sutton, W.R., Srivastava, J.P., & Neumann, J.E. (2013). *Looking beyond the horizon : how climate change impacts and adaptation responses will reshape agriculture in Eastern Europe and Central Asia. Directions in development: agriculture and rural development.* Washington DC: World Bank.

Swenson, J.J., Carter, C.E., Domec, J.C and Delgado, C.I. (2011) Gold mining in the Peruvian Amazon: Global prices, deforestation, and mercury imports. *PLoS ONE* 6(4): e18875.

Swingle, W.T. and Reece, P.C. (1943) Botany of Citrus. In: Webber, L and Batchelor, H. (eds.), *The Citrus Industry, vol. 1.* University of California Press, Berkeley. Pp. 129–474.

Tanaka, T. (1977) Fundamental discussion of Citrus classification. *Studies in Citrology* 14: 1–6.

Tanksley, S.D. and McCouch, S.R. (1997) Seed Banks and Molecular Maps: Unlocking Genetic Potential from the Wild. *Science* 277: 1063–1066.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siquira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. and Williams, S.E. (2004) Extinction risk from climate change. *Nature* 427: 145–148.

Tilman, D., Balzer, C. Hill, J. and Befort, B.L. (2011) Global food demand and the sustainable intensification of agriculture. *PNAS* 108: 20260–20264.

Tropicos (2011) Tropicos.org. Missouri Botanical Garden. [online] Available at: http://www.tropicos.org/ (Accessed 1 April 2011).

The Trussell Trust (2015) UK Foodbank statistics for 1st April 2014 - 31st March 2015. [online] Available at: http://www.trusselltrust.org/stats (Accessed 16 November 2015).

Tubiello, F.N, Salvatore, M., Cóndor Golec, R.D., Ferrara, A., Rossi, S., Biancalani, R., Federici, S., Jacobs, H. and Flammini, A. (2014) *Agriculture, Forestry and Other Land Use Emissions by Sources and Removals by Sinks: 1990 – 2011 Analysis*. ESS Working Paper No. 2. FAO, Rome.

Tyack, N. and Dempewolf, H. (2015) The economics of crop wild relatives under climate change. In: Redden, R., Yadav, S.S, Maxted, N., Dulloo, M.E., Guarino, L. and Smith, P. (eds.) *Crop wild relatives and climate change*. Wiley-Blackwell, Hoboken, New Jersey, USA. Pp. 281–291.

Uleberg, E., Hanssen-Bauer, I., van Oort, B. and Dalmannsdottir, S. (2014) Impact of climate change on agriculture in Northern Norway and potential strategies for adaptation. *Climatic change* 122(1-2): 27–39.

UN (2011) *World Population Prospects*, UN Department of Economic and Social Affairs, Population Division, New York. [online] Available at: http://esa.un.org/unpd/wpp/index.htm (Accessed 11 January 2012).

United Nations (2013) *World Population Prospects: The 2012 Revision*. Population Division, Dept. of Economic and Social Affairs, United Nations, New York.

United Nations (2015*) World Population Prospects: The 2015 Revision*, *Key Findings and Advance Tables.* Working Paper No. ESA/P/WP.241.

United Nations (2016) Sustainable Development Goals: 17 goals to transform our world. [online] Available at: http://www.un.org/sustainabledevelopment/ (Accessed 10 May 2016).

UNEP-WCMC (2013) Centres of Plant Diversity. Version 1.0 (digital reproduction of Centres of Plant Diversity, S.D. Davis, V.H. Heywood & A.C. Hamilton (eds.), WWF and IUCN, Gland, Switzerland, 1994-7).

Ureta, C., Martínez-Meyer, E., Perales, H.R. and Álvarez-Buylla, E.R. (2012) Projecting the effects of climate change on the distribution of maize races and their wild relatives in Mexico. *Global Change Biology* 18(3): 1073–1082.

USDA (2011) Germplasm Resources Information Network – (GRIN) [Online Database]. National Germplasm Resources Laboratory, Beltsville, Maryland. [online] Available at: http://www.ars-grin.gov/cgi-bin/npgs/html/queries.pl (Accessed 1 April 2011).

USDA (2014) USDA Forest Service and Agricultural Research Service Strategy for the Complementary Conservation of Wild Cranberry (Vaccinium macrocarpon Ait. and V. oxycoccos) Genetic Resources and Protocols for Collecting Genetic Material, Germplasm, and Herbarium Vouchers. [online] Available at:

http://www.fs.fed.us/wildflowers/ethnobotany/documents/cwr/StrategyProtocolsComplementaryConservationWildCranberry08192014.pdf.

van de Wouw, M, Kik, C. van Hintum, T., van Treuren, R. and Visser, B. (2009) Genetic erosion in crops: concept, research results and challenges. *Plant Genetic Resources: Characterization and Utilization* 8(1): 1–15.

Vavilov, N.I. (1926) The centres of origin of cultivated plants. *Works of Applied Botany and Plant Breeding* 16: 248.

Vavilov, N.I. (1935) The phytogeographical basis for plant breeding. *Theoretical Basis for Plant Breeding* 1: 17–75.

Vavilov, N.I. (1940) The theory of the origin of cultivated plants after Darwin. *Nauka (Science)* 2: 55–75.

Vavilov, N.I. (1992) *Origin and Geography of Cultivated Plants* (Dorofeev, V.F., ed.). Cambridge University Press, Cambridge, UK.

Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H.M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H.P., Rondinini, C., Smith, R.J., Venter, M. and Watson, J.E.M. (2014) Targeting Global Protected Area Expansion for Imperiled Biodiversity. *PLoS Biology* 12(6): e1001891. doi:10.1371/journal.pbio.1001891.

Villard, M.-A. and Jonsson, B.G. (eds.) (2009) *Setting conservation targets for managed forest landscapes*. Cambridge University Press, Cambridge.

Vincent, H., von Bothmer, R., Knüpffer, H., Amri, A., Konopka, J. and Maxted, N. (2012) Genetic gap analysis of wild Hordeum taxa. Plant *Genetic Resources Characterization and Utilization* 10 (3): 242–253.

Vincent, H., Wiersema, J., Kell, S., Fielder, H., Dobbie, S., Castañeda-Álvarez, N.P., Guarino, L., Eastwood, R., León, B. and Maxted, N. (2013) A prioritized crop wild relative inventory to help underpin global food security. *Biological Conservation* 167: 265–275.

Vollbrecht, E. and Sigmon, B. (2005) Amazing grass: developmental genetics of maize domestication. Biochemical Society Transactions 33: 1502–1506.

Yadav, S.S., Redden, R., Hatfield, J.L., Lotze-Campen, H. and Hall, A. (eds.) (2011) *Crop Adaptation to Climate Change.* Wiley-Blackwell, Chichester.

Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T. and Gittleman, J.L. (2013) Targeting global conservation funding to limit immediate biodiversity declines. *PNAS* 110(29): 12144–12148.

Warschefsky, E., Penmetsa, R.V., Cook, D.R. and von Wettberg, E.J. (2014) Back to the wilds: tapping evolutionary adaptations for resilient crops through systematic hybridization with crop wild relatives. *American Journal of Botany* 101(10):.1791–1800.

WCSP (2015) World Checklist of Selected Plant Families. Facilitated by the Royal Botanic Gardens, Kew. [online] Available at: http://apps.kew.org/wcsp/ (Accessed 29 January 2015).

Wellington, G.M., Glynn, P.W., Strong, A.E., Navarrete, S.A., Wieters, E. and Hubbard, D. (2001) Crisis on coral reefs linked to climate change. *Eos, Transactions American Geophysical Union* 82(1): 1–5.

Wicke, B., Sikkema, R., Dornburg, V., and Faaij, A. (2011). Exploring land use changes and the role of palm oil production in Indonesia and Malaysia. *Land Use Policy* 28(1): 193–206.

Wiersema, J.H., León, B. and Garvey, E.J. (2012) Identifying wild relatives of subtropical and temperate fruit and nut crops. Acta Horticulturae 948: 285–288.

WWF (2015) *Hidden Himalayas: Asia's Wonderland: New species discoveries in the Eastern Himalayas, Volume II, 2009-2014*. WWF-World Wide Fund for Nature, Switzerland.

WWF (2016) *Protecting people through nature: natural world heritage sites as drivers of sustainable development*. World Wide Fund for Nature (Formerly World Wildlife Fund), Gland, Switzerland.

Zeven, A.C. and Zhukovsky, P.M. (1975) *Dictionary of cultivated plants and their centres of diversity*. Pudoc, Wageningen, the Netherlands.

Zhang, X., Zhou, S., Fu, Y., Su, Z., Wang, X. and Sun, C. (2006) Identification of a drought tolerant introgression line derived from Dongxiang common wild rice (Oryza rufipogon Griff.). *Plant Molecular Biology* 62: 247–259.

APPENDIX 1

An approach for *in situ* gap analysis and conservation planning on a global scale

This chapter has been published as:

Vincent, H., Castañeda-Álvarez, N.P., Maxted, N. (2016) An approach for *in situ* gap analysis and conservation planning on a global scale. In: Maxted, N., Ehsan Dulloo, M. and Ford-Lloyd, B.V. (eds.) *Enhancing Crop Genepool Use: Capturing Wild Relative and Landrace Diversity for Crop Improvement*. CAB International, Wallingford, UK. ISBN-13: 978-1-78064-613-8.

Author contributions:

Conceived and designed the study: **HV**

Data collection and preparation: **HV**

Creation of database: **HV**

Performed analysis: **HV**

Analysed results: **HV**

Wrote the paper: **HV**

Critically reviewed the paper: **HV**, NM

A1.1 Introduction

With the human population estimated to reach 9.6 billion by 2050 (United Nations, 2013), the increase in demand for food, combined with: climate change, predicted increases in extreme weather events, reduced availability of natural resources and an increasingly animal based diet globally, is likely to overwhelm the current agricultural system (Godfray *et al.*, 2010; Kastner *et al.* 2012). Furthermore, as climate change is predicted to reduce food crop production by up to 2 % per decade until the end of the 21st century (Porter *et al.*, 2014); existing agricultural practices will need to adapt to ensure food future security (FAO *et al.*, 2013). These adaptations include reducing food wastage, effective sustainable management of natural resources, sustainable intensification of current food systems and improving current crop varieties to withstand changing climates and prevent reduction in yield (Godfray *et al.* 2010; Tilman *et al.* 2011).

Crop wild relatives (CWR) are a vast repository of genetic traits that have been successfully used to improve traditional crops and could, if used more systematically, help to diversify and adapt current crop varieties to ensure future food security (McCouch *et al.* 2013). CWR are being increasingly utilised as gene donors in plant breeding programmes (Maxted and Kell, 2009), having been used to improve a number of crop attributes including: nutritional quality (Sebolt *et al.,* 2000; Nassar, 2003), resistance to biotic and abiotic stresses (Panella and Lewellen, 2007) and yield (Jordan *et al.*, 2004; Brar, 2005). However, despite their importance and increasing popularity within crop improvement, CWR are poorly conserved globally (Heywood and Dulloo, 2005; Maxted and Kell, 2009; Dias *et al.*, 2012) and, like the majority of wild plants, threatened with increased risk of extinction due to damaging anthropogenic activities, including human induced climate change (Jarvis *et al.*, 2008; Kell *et al.*, 2012).

With both the CBD and FAO explicitly stating the importance of global conservation and utilisation of CWR for agriculture in: Aichi Target 13 (CBD, 2010b), the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) (FAO, 2001) and the CBD Global Strategy for Plant Conservation 2011–2020 (CBD, 2010a); the need for a systematic conservation strategy for the wild relatives of the World's most important crops is paramount. To address this conservation need, a ten year initiative – "Adapting agriculture to climate change: collecting, protecting and preparing the crop wild relatives" – was launched, led by the Global Crop Diversity Trust (GCDT) and the Millennium Seed Bank, Kew (GCDT, 2011). The initiative involves: identifying priority CWR related to the World's most important crops (Vincent *et al.*, 2013); *ex situ* gap analysis to determine novel potential areas Worldwide for priority CWR sampling (Castañeda-Álvarez *et al.*, 2016; Chapter 12, this volume); *in situ* gap analysis to clarify key regions and existing protected areas for the development of multi-crop CWR genetic reserves; focused CWR germplasm collection and storage in seed genebanks; characterisation of novel germplasm and development of pre-breeding lines for testing and evaluation; dissemination of knowledge and genetic material to plant breeders, researchers and other users of plant genetic resources (PGR) (Dempewolf *et al.,* 2014).

In situ CWR conservation plays a vital role in complementary conservation, alongside *ex situ* activities, as it allows wild populations to continue adapting to a changing environment and evolve new traits which might prove useful in plant breeding. Historically, *in situ* conservation has been overlooked due to the larger upfront costs involved, longer term project commitments, lack of funding and difficulties securing and monitoring genetic reserves, but hopefully with increased advocacy by major biodiversity organisations and growing awareness of the importance of complementary conservation of these species and their habitats, CWR *in situ* conservation will receive the attention it deserves.

Gap analysis is an established and widely used technique in CWR conservation which enables thorough assessment of the efficacy of the current conservation framework and identification of taxa, intra-taxon genetic diversity, and geographical sites that are under-represented and require additional conservation action (Maxted *et al.*, 2008b; Maxted and Kell, 2009; Ramírez-Villegas *et al.*, 2010; Maxted *et al.,* 2011a; Parra-Quijano *et al.*, 2012a). However, the majority of gap analysis techniques developed for PGR and CWR conservation are targeted at *ex situ* conservation and comparatively *in situ* gap analysis has been left somewhat underdeveloped. This chapter attempts to help address this gap by providing an overview of the methodologies and research associated with *in situ* gap analysis of global priority CWR taxa; readers are referred to Vincent *et al.* (Chapter 3, this thesis) for full details.

A1.2 Methodology

Successful *in situ* conservation planning consists of the following basic steps: (a) circumscription of target taxon and target area; (b) evaluating current conservation actions; (c) setting conservation targets; (d) ensuring persistence in targeted taxa through conservation efforts; (e) selecting and designing a network of reserves; and (f) setting priorities for action amongst conservation areas (Groves, 2003). This general framework has been adapted and developed over recent years to apply to the specific needs of CWR conservation (Iriondo *et al.*, 2008; Maxted *et al.*, 2008b; Hunter and Heywood, 2011; Maxted *et al.,* 2011b; Vincent *et al.*, Chapter 3 this thesis).

The methodology utilised for the global CWR *in situ* gap analysis, was further expanded to eight steps: (a) determining target taxa and scope; (b) eco-geographic conspectus; (c) analysis of genetic diversity data; (d) evaluating current *in situ* conservation actions; (e) analysis of projected climate change impacts; (f) reserve selection; (g) setting priorities amongst conservation areas; and (h) expert feedback. The detailed methodology description presented below is extracted from Vincent et *al.* (Chapter 3, this thesis).

A1.2.1 Determining target taxa and scope

Setting a clear goal for conservation efforts is an essential first step in gap analysis and conservation planning in general. This often requires meeting with project partners and stakeholders to fully discuss the project requirements and goals. The taxa and geographic area intended for inclusion in gap analysis can be clarified in many ways, from being directly stated as part of a specific programme to conserve a particular species, to the need for further elucidation as part of a broader project. Depending on the scope (i.e. local, national, regional or global), various sources of information should be consulted in order to determine the CWR taxa that will be considered in the gap analysis, for example: analyses at the local and national scale can benefit from published CWR inventories, as is the case for Benin (Idohou *et al.,* 2012), Portugal (Magos Brehm *et al.,* 2008), USA (Khoury *et al*., 2013), and Venezuela

(Berlingeri and Crespo, 2012). Online sites, like the Crop Wild Relatives Global Portal (2015) which contains information, reports and books from previous projects that deal with the identification of CWR taxa at the national level in multiple countries, can also help to elucidate target taxa for a particular country. In addition, this information can be complemented with The Harlan and de Wet Inventory (http://www.cwrdiversity.org/checklist/), which lists the CWR associated with the World's most important food crops (Vincent *et al*., 2013).

Prioritisation is a key technique in defining a set of target CWR taxa for conservation, especially when working from a national inventory or a large geographical area of interest. Maxted *et al.* (1997b) and Magos Brehm *et al.* (2010) describe several criteria, along with the benefits and pitfalls of each, for CWR prioritisation, these include: economic value, legislation, ethnobotanical value, threat assessment and current conservation status. Furthermore, local and national analyses may only consider native CWR, thus it is necessary to check the native distribution for each taxon; this information can found in The Harlan and de Wet Inventory for CWR associated with globally important crops, along with other sources such as the Germplasm Resources Information Network (GRIN, 2015) and the World Checklist of Selected Plant Families (WCSP, 2015).

A1.2.2 Eco-geographic conspectus

Once the final list of target taxa is ready for inclusion in the gap analysis it is necessary to begin accumulating data for each CWR. Passport data for target taxa occurrences can be obtained from a wide range of sources including major herbariums worldwide, seed gene bank databases, expert's personally collected data and online databases. The data should then be collated and organised in a single database, preferably following standards that will ensure the interoperability of the dataset with external requesters (Castañeda Álvarez *et al.,* 2011). The quality of the data gathered needs to be assessed and checked thoroughly to remove obvious misplaced records, calculate coordinates where locality descriptions are available and of good quality, and standardise CWR nomenclature following a particular taxonomic system.

Examples of online repositories where occurrence records can be obtained are: the Global Biodiversity Information Facility (http://www.gbif.org/), Genesys – the gateway to genetic resources (https://www.genesys-pgr.org/), the European Cooperative Programme for Plant Genetic Resources database (http://eurisco.ipk-gatersleben.de/) and the global CWR occurrence dataset, which will be available soon for download (Castañeda Álvarez *et al.*, 2016b).

Information on breeding systems of target taxa should also be collected either from experts or literature as it can help to plan how many populations will be targeted in the reserve selection software to ensure persistence. Finally, it is important to gather any genetic diversity information for each target taxon, so that the reserve selection software can aim to conserve as much of the infra-specific diversity of each priority CWR as possible.

A1.2.3 Analysis of genetic diversity data

Before the current conservation status of the target CWR is evaluated, it is important to examine any genetic diversity data that may be available. Individual germplasm and herbarium records may have this data, as is the case for tomato (http://www.kazusa.or.jp/tomato/), rice (http://www.oryzasnp.org/), maize (http://www.panzea.org/) and wheat (http://www.cerealsdb.uk.net/). These resources enable *in silico* analysis that can potentially increase understanding of the genetic structure of CWR populations, thus identifying geographical areas with high genetic diversity and/or unique genes that can be targeted for conservation. Ideally, monitoring the genetic composition of CWR populations should be undertaken to help to detect whether genetic erosion processes are taking place, and information obtained fed back into conservation efforts (Marfil *et al.,* 2015).

Despite the usefulness of genetic information to inform conservation needs, many CWR taxa are still lacking this kind of information. In such cases, environmental adaptation can be used as a proxy for genetic diversity. Ecogeographic land characterisation (ELC) maps cluster edaphic, geophysical and climatic variables to qualify land into categories that represent different environmental niches. When overlaid with taxa occurrences, it is possible to determine how many environmental niches each taxon exists in, which can act as a substitute for infra specific diversity. Parra-Quijano *et al.* (2012a) developed this technique for CWR and successfully applied it to collect germplasm of six *Lupinus* species located in Spain from various environmental niches identified by an ELC map (Parra-Quijano *et al*., 2012b). This helped to increase both genetic and geographic representativeness of genebank collections of those species. This method can also be applied to *in situ* conservation, as reserve selection algorithms can be set to conserve instances of each CWR/environmental niche combination. To aid conservation planners, Parra-Quijano *et al.* (2014) have developed 'ELC Mapas'; a program which creates an ELC map for a defined geographical area via user defined environmental inputs.

A1.2.4 Evaluating current *in situ* conservation actions

To assess current *in situ* conservation actions, it is recommended to compare the distribution and passport data of each target taxon to the spatial extent of existing Protected Areas (PA). There are many available sources of PA geospatial data at varying levels of detail, examples of which include:

- Global: Protected Planet, previously the World Database on Protected Areas (WDPA) (http://www.protectedplanet.net/)
- Regional: European Environmental Agency (http://www.eea.europa.eu/data-and-maps/data/natura-5)
- National: Protected Areas Database of the United States (PAD-US) (http://gapanalysis.usgs.gov/padus/data/download/)
- National: Protected Areas of South Africa (http://bgis.sanbi.org/protectedareas/protectedAreas.asp)

Non-terrestrial PAs should be removed and the extent of each remaining PA overlaid with geo-referenced accession and herbarium passport data. Then using GIS, overlaps between taxon occurrence points and PAs can be recorded to determine the current conservation status of each taxon and priority CWR as a whole. Also, following on from step A1.2.3, it will be possible to determine how much genetic diversity of each individual taxon is currently represented in the existing PA network, particularly when using ELC maps.

As this process only identifies taxa that may be passively being conserved, it is advisable to check with the management plans of each PA containing target taxa records to ascertain whether they are mentioned explicitly. However, management plans for sites worldwide are rarely available to researchers so it is usual practice to assume only passive conservation is occurring.

A1.2.5 Analysis of projected climate change impacts

As *in situ* conservation, in the majority of cases, is a long term commitment, it is important to ensure that the populations of target taxa chosen for conservation are likely to persist. Therefore before establishing a reserve it is advisable to model the threats that compromise the long term persistence of taxa populations such as mining, urbanisation, animal grazing and climate change. The impact of most threats that may negatively affect CWR taxa habitats can be reduced by implementing management plans collectively with stakeholder participation and even introducing protective legislation on a national or global level. This is not the case for climate change which cannot be locally mitigated, therefore, understanding the potential impacts of climate change on CWR distributions is a critical step during reserve planning to ensure the CWR populations conserved are those most likely to persist over time. Jarvis *et al.* (2008) modelled the current and future potential distributions of CWR associated with peanut (*Arachis hypogaea* L.), potato (*Solanum tuberosum* L.) and *Vigna* Savi species using the Bioclim climate envelope. These models, when compared, predicted high fragmentation in the current habitats of CWR and major reductions in habitat range, thus highlighting the need for climate change mitigation within conservation strategies.

Climate change projections are freely available for different future time points (i.e. 2020, 2050, 2100), for the four Representativeness Concentration Pathways (RCPs), as per the IPCC fifth assessment report (http://cmip-pcmdi.llnl.gov/cmip5/), and for multiple General Circulation models (GCM). For instance, the WorldClim website holds freely available future climate data, downscaled and calibrated using the current scenario of Worldclim (Hijmans *et al.*, 2005), including raster files of Bioclim variables (http://www.worldclim.org/CMIP5). The future climate models can be used to assess whether particular grid cells/sites will still be stable long term for target taxa or to assess taxa data points individually for significant change which would mean that population would likely perish.

A1.2.6 Reserve selection

Before selecting sites for genetic reserves it is important to set targets for conservation. This can be a percentage of a certain ecosystem, a fixed number of target taxa occurrences, or a proportion of a taxon's distributional range. One method of setting targets is to analyse the breeding system of each taxon and determine the minimum number of populations needed to ensure persistence *in situ*; expert advice would be beneficial in this case. A more simple method suggested by Brown and Briggs (1991) and supported by Dulloo *et al.* (2008) is to conserve a minimum of 5 populations per taxon throughout its range.

When designing a network of reserves it is typical to run the geo-referenced occurrence records through a reserve selection algorithm to produce an ideal group of sites that fulfils all conservation targets, which can serve as a starting point for discussions with experts and land managers. There are many reserve selection algorithms available online that can assist in choosing sites for conservation, whilst meeting complex conservation targets, several of which are free to use. One widely used algorithm in CWR conservation planning is the Rebelo complementarity analysis (Rebelo and Siegfried 1990; 1992) feature in DIVA-GIS (Hijmans *et al.*, 2001), which selects taxon rich sites based upon the taxa that have not yet been selected by previous iterations. However, this algorithm lacks flexibility in terms of setting targets for individual taxa and there are other algorithms and programs that can offer more thorough data analysis. These sophisticated programs include:

- Marxan (http://www.uq.edu.au/marxan/get-marxan-software)
- Zonation (http://cbig.it.helsinki.fi/software/zonation/)
- ConsNet (http://uts.cc.utexas.edu/~consbio/Cons/consnet_home.html)

Marxan is a flexible tool that attempts to solve the minimum set reserve problem using simulated annealing; it can be run with both taxon co-ordinate occurrence data and polygons of species distribution. Marxan can also analyse different scenarios whilst offering options to weight species due to rarity or relative importance, set targets for the minimum number of occurrences for each taxon to be achieved in the whole network and set costs for each potential planning unit. Zonation is similar to Marxan, but operates by iteratively removing the least valuable cell/site whilst matching this with the overall complementarity and connectivity of the total solution. Zonation also allows the use of point data and raster data as inputs. ConsNet is software that uses smart heuristic searches to find reserve solutions that best meet the criteria of the conservation planners. It has many possible user inputs such as costings of cells/sites and different search options, such as minimum area search and maximum representation search. All of these programs require some experimentation with different user settings to produce significant results.

When using reserve selection algorithms many projects run only the complete dataset, however, it is necessary to run several scenarios on subsets of the data. It is particularly important to analyse the taxon occurrence points that fall within PAs separately from those not protected or at least factor the presence of PAs into site costs in full data runs. This is due to it being easier to set up genetic reserves in existing PAs, rather than acquire land for new sites.

A1.2.7 Setting priorities amongst conservation areas

Usually it is not possible to establish a complete network of reserves due to economic, political or other restraints. Therefore it is necessary to prioritise sites from the ideal network for *in situ* conservation action. One method for prioritising sites is to compare complementarity runs against the complete reserve network to determine which sites will provide the most CWR richness. Further sites can be prioritised based upon the cost of site, threats and priority species (such as Annex 1 food crops of the ITPGRFA); further prioritisation techniques are described by Magos Brehm *et al.* (2010). The presence of other important biodiversity, or overlap with Myers or Vavilov hotspots may also be good rationale for prioritising sites, as this may help persuade conservation agencies and relevant authorities to set up sites if there is overall high biodiversity, not just CWR diversity.

A1.2.8 Expert feedback

If the goal is to establish a complete network of reserves, experience has shown this will only be possible with full stakeholder buy-in (Maxted *et al.*, 2008c), therefore it is important to involve stakeholders throughout each stage of conservation planning. However, the first complete 'ideal' run of a reserve selection programme is a key time to get stakeholder feedback and expert input. This will provide a basis for discussion on potential sites, priorities and whether they are practically feasible sites for genetic reserves. These discussions can lead back to further reserve planning software runs, as there will often be a need to compromise between the best possible solution as determined by the reserve selection algorithm and the requirements of the stakeholders.

A1.3 Summary of global *in situ* gap analysis

A global *in situ* gap analysis for the CWR of 173 crop gene pools, as listed in the Harlan and de Wet Inventory (Vincent *et al.* 2013), was undertaken to identify an ideal worldwide network of genetic reserves which maximises the number of priority CWR conserved *in situ*. The global CWR occurrence database (Castañeda Álvarez *et al.*, 2016b) was edited to include only records related to target CWR; non-native and poorly geo-referenced records were also removed leaving occurrence data for 1158 priority species. A generalised ELC map was produced for the whole terrestrial World at the 20km x 20km resolution, using the ELC Mapas tool developed by Parra-Quijano *et al.* (2014). The geo-referenced data was overlaid on the ELC map to extract the environmental niche for each occurrence point, resulting in 6236 unique CWR/environmental niche combinations. PA data was obtained from the World

Database on Protected Areas (WDPA) as a geospatial database (IUCN and UNEP-WCMC, 2012) and a shapefile for the Natura 2000 sites was also obtained (European Environment Agency, 2013) as this important dataset was not included in the WDPA. The PA files were edited to remove non-terrestrial PAs, then overlaps between taxon points and PAs were recorded to determine the current, albeit passive, conservation status of each population, taxon and priority CWR as a whole. During the timeframe of this study it was not possible to contact all the PA managers where CWR appeared to exist, therefore it was assumed there was no active management of CWR in these PAs. 19 GCMs for the year 2070 with RCP 45 were downloaded from the Worldclim website as Bioclim rasters and combined to determine which taxa would be most likely to survive predicted climate change. Marxan was used to model different scenarios for conserving subsets of the priority CWR taxa, with the aim of discovering the best sites for multiple crop CWR conservation with priority for sites that were potentially tolerant to climate change and overlapped with PAs. Target numbers of populations to conserve were set as 5 per individual taxon as recommended by Dulloo *et al.* (2008). However, during analysis of the ELC categories per taxon, a target of only 1 per ELC/individual species combination was studied, due to their large number. Marxan scenarios were run for:

- All taxa
- All Gene pool 1B (GP1B) taxa
- All taxa related to ITPGRFA Annex1 food crops
- All GP1B taxa related to ITPGRFA Annex1 food crops
- All ELC/taxa combinations
- All GP1B ELC/taxa combinations

- All ELC/taxa combinations related to ITPGRFA Annex1 food crops
- All GP1B ELC/taxa combinations related to ITPGRFA Annex1 food crops

Finally, Rebelo complementary analysis was run on the final Marxan reserve solutions to further prioritise a set of top 50 sites worldwide which would conserve maximal amounts of taxa diversity.

The gap analysis found that 403 of the 1158 studied species, including four whole genera, had fewer than 10 good quality occurrence records, which is the minimum number of records needed to reliably produce a gap analysis assessment. Out of the remaining 755 CWR species, the gap analysis found that 129 CWR are not found in a single PA, with 20 of these being primary gene pool species. Additionally, over 50% of the assessable species have less than 10% of their occurrence records within PAs, suggesting a poor level of overlap between CWR and protected area occurrence and therefore, at least, passive *in situ* conservation. In terms of genetic diversity, 434 of the assessable species have less than 50% of their associated environmental niches found in PAs; however 84 species have all of their niches represented in the existing PA network. Worryingly, only 104 of the 1158 priority CWR have been assessed by the IUCN Red List (IUCN, 2015), leaving the conservation status of these species unknown.

Figure 10.1 shows the best Marxan solution for all priority CWR of the 173 globally important crops studied in the gap analysis, whilst Figure 10.2 highlights the top 50 complementary sites from the same scenario. The richest complementary CWR site was found on the Israel/Jordan/Palestine/Syria border and contained 61 unique CWR species from 20 genera. The remaining top 10 sites of importance were as follows: the southern Armenia/Azerbaijan border (53 CWR from 23 genera); Virginia, USA (30 CWR from 11 genera); southern Madrid, Spain (52 CWR from 25 genera); Rajasthan, India (24 CWR from 17 genera); Mexico state, Mexico (24 CWR from 12 genera); Moungo, Cameroon (17 CWR from 9 genera); Java, Indonesia (20 CWR from 10 genera); Brasilia region, Brazil (18 CWR from 6 genera); and Cajamarca, Peru (16 CWR from 2 genera). Out of the top 10 complementary sites, all overlap with PAs except those in Rajasthan, India and Java, Indonesia; these two sites require urgent ground-truthing to confirm the presence of CWR and to formulate *in situ* conservation strategies outside of the PA network. All of the top 10 sites should be a priority for establishing new reserves or at the very least, careful and regular monitoring of populations, their health and threats.

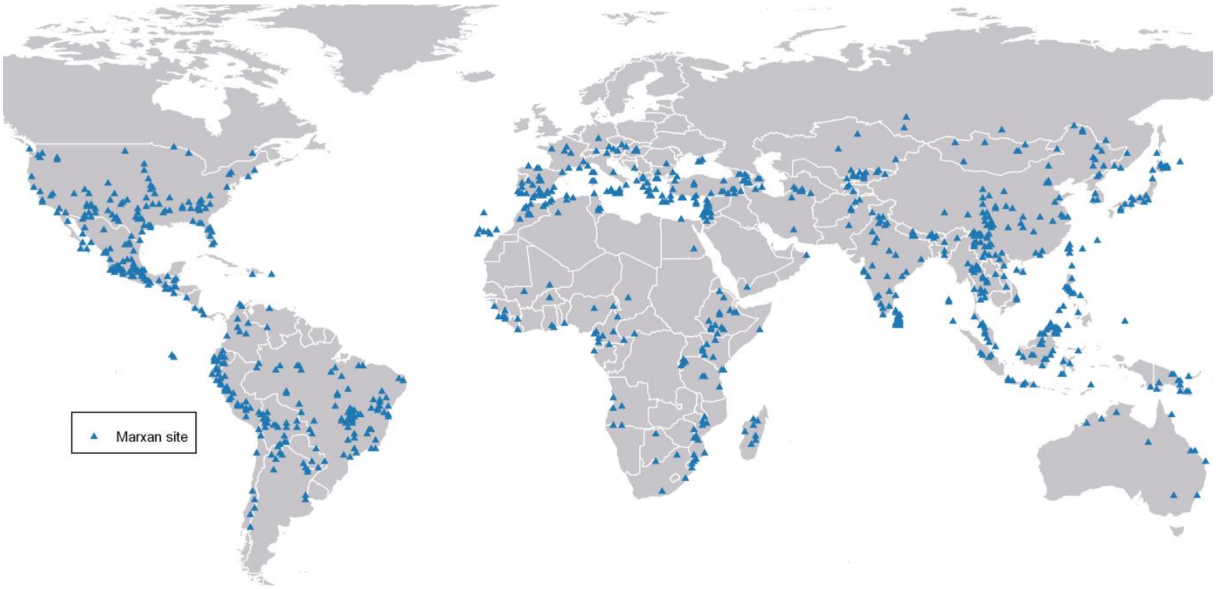

Figure A1.1 Best Marxan solution for all priority CWRs of 173 globally important crops.

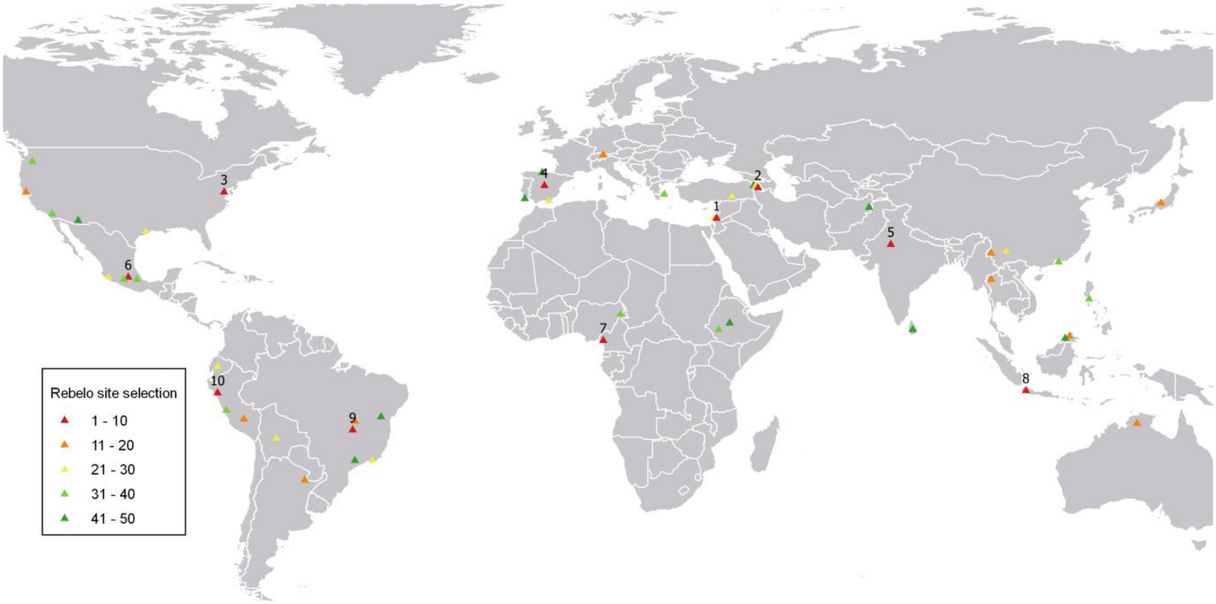

Figure A1.2 Top 50 complementary sites from the ‘all priority CWR’ best solution.