

**University of São Paulo
“Luiz de Queiroz” College of Agriculture**

**Climatic niches and geographical ranges of sugarcane wild relatives: a
comparative and evolutionary approach**

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Dissertation presented to obtain the degree of Master
in Science. Area: Genetics and Plant Breeding

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RESUMO

Nichos climáticos e amplitudes geográficas de parentes selvagens de cana-de-açúcar: um enfoque comparativo e evolutivo

A distribuição das espécies é resultado da interação entre seus atributos ecológicos e forças evolutivas, aspectos que são estudados pelas biogeografia ecológica e histórica, respectivamente. Apesar de haver uma separação histórica entre essas duas áreas, a aplicação do conceito de nicho ecológico na modelagem de nichos ecológicos e distribuição de espécies tem permitido uma maior integração entre ambas. Os resultados dessa integração têm permitido o preenchimento de diversas lacunas no conhecimento científico sobre a biodiversidade. Essas lacunas são especialmente relevantes para um grupo de plantas conhecido como parentes selvagens de plantas cultivadas (PSPCs), que são um recurso genético valioso com um papel crucial na garantia da segurança alimentar. Nesta dissertação, nós usamos dados de ocorrência e variáveis bioclimáticas para modelar a distribuição geográfica potencial de 15 espécies de parentes selvagens da cana-de-açúcar, assim como para caracterizar seus nichos climáticos em um espaço ambiental bidimensional. Uma filogenia, recentemente publicada, foi reconstruída e utilizada para investigar os mecanismos evolutivos que moldaram a geografia da especiação e a evolução dos nichos climáticos nesse grupo. A modelagem da distribuição potencial das espécies mostrou que os parentes selvagens da cana-de-açúcar são potencialmente distribuídos pelo globo. Adicionalmente, os modelos produzidos podem ser utilizados para informar futuras expedições de coleta, já que os parentes da cana são um dos menos representados em bancos de germoplasma. Espécies mais próximas filogeneticamente exibiram um alto grau de simpatria e assimetria de distribuições, enquanto espécies mais distantes ocorrem em total alopatria. Além disso, foi encontrada uma correlação negativa, e estatisticamente significativa, entre o tempo de divergência dos clados e o nível de simpatria, sugerindo que a atual distribuição geográfica dessas espécies pode ter resultado de dispersão de longa distância seguido por eventos de especiação simpátrica recentes. A caracterização dos nichos mostrou que variáveis relacionadas a temperatura mínima e aridez são aquelas que mais contribuem para a variação entre os nichos climáticos das espécies. A maioria das espécies possuem nichos climáticos restritos, enquanto duas apresentam nichos climáticos amplos. Em geral, os nichos climáticos de parentes selvagens da cana-de-açúcar não são idênticos e o nível de similaridade entre eles é o mesmo que o esperado ao acaso, apesar de espécies mais próximas apresentarem os maiores níveis de sobreposição de nicho. Adicionalmente, os modelos evolutivos sugerem que diferentes processos atuaram para moldar as tolerâncias climáticas dessas espécies, a dimensão do nicho climático relacionado à temperatura foi melhor modelada pelo modelo Ornstein-Uhlenbeck com dois ótimos e a dimensão relacionada à aridez foi melhor modelada por um modelo de movimento Browniano. Portanto, nosso estudo mostra a importância de utilizar dados já disponíveis para analisar os atributos ecológicos e aspectos da evolução de PSPCs, que podem ser utilizados para fomentar iniciativas de conservação e para o uso mais eficiente destas espécies no melhoramento de plantas.

Palavras-chave: Parentes Selvagens da Cana-de-açúcar, Nicho Climático, Distribuição Geográfica

ABSTRACT

Climatic niches and geographical ranges of sugarcane wild relatives: a comparative and evolutionary approach

Species distributions are the result of the interplay between ecological requirements and evolutionary mechanisms, which are studied by ecological and historical biogeography, respectively. Although these fields have been historically separate, the concept of ecological niche has allowed their integration. The modelling of ecological niches and species distributions in light of the evolutionary processes has allowed the filling of considerable gaps of scientific knowledge about biodiversity. These gaps are especially relevant for a group of plants known as crop wild relatives (CWR), which are a valuable genetic resource with a crucial role in guaranteeing food security. In this dissertation, we used available occurrence data and bioclimatic variables to model the potential geographic distribution of 15 species of the sugarcane relatives and to characterize their niches in a bidimensional environmental space. We also reconstructed a recently published phylogeny and used it to investigate the predominant mechanism of speciation and the mechanisms shaping niche evolution in the group. The results showed that sugarcane relatives are potentially distributed worldwide and that range models can be used to inform future collection expeditions, considering that the relatives of this crop is one of the most underrepresented in genebanks. Closely related species show a high degree of sympatry with asymmetrical ranges, whilst species from different clades occur in total allopatry. We found a significant negative correlation between age of divergence between clades and pairwise level of sympatry, which suggests that the current geographical distribution may be a result of long-distance dispersion followed by recent events of sympatric speciation. Characterization of niches showed that climatic variables related to minimum temperatures and aridity were the ones that most contributed to variation among climatic niches of these species. Whilst most species show narrow climatic niches, two show a very broad niche. In general, sugarcane relatives' climatic niches are not identical and are just similar as expected by chance, even though closely related species showed the highest levels of niche overlap. Additionally, models of evolution suggests that different processes acted to shape the climatic tolerances of sugarcane wild relatives, the first dimension of climatic niches related to minimum temperature was best modelled by a Ornstein-Uhlenbeck model with two optima and the dimension related to aridity is best modelled by a Brownian Motion model. Therefore, our study shows the importance of using already available data to analyse the ecological attributes and evolutionary aspects of CWR, which can be used to foment conservation initiatives and a more efficient use of these species in breeding.

Keywords: Sugarcane Wild Relatives, Climatic Niches, Geographical Ranges

1 CLIMATIC NICHES AND GEOGRAPHICAL RANGES OF SUGARCANE WILD RELATIVES: A COMPARATIVE AND EVOLUTIONARY APPROACH

Abstract

Crop wild relatives (CWR) are a potential source of alleles related to abiotic and biotic stress, thus, valuable for plant breeding. Despite their importance, CWR use in plant breeding research programs is hindered by the lack of knowledge of their distribution, abiotic tolerances and the mechanisms underlying their diversification. Sugarcane is one of the most important sources of carbohydrates for human consumption and one of the most relevant bioenergy crops; however, knowledge about their wild relatives is still scarce. In this context, we used occurrence data of 15 sugarcane wild relatives along with 19 bioclimatic variables to model their potential geographic distribution and characterize their climatic niches, in a bidimensional environmental space. We also used a recently published phylogeny to investigate the geography of speciation and the macroevolutionary forces shaping the diversification of climatic niches in this group. Our ecological niche models showed that sugarcane relatives are distributed worldwide and that closely related species tend to occur in sympatry and present asymmetrical ranges and that more distantly related species occur in allopatry. We found that the level of sympatry in this group is negatively correlated with divergence events, suggesting that speciation probably occurred by sympatric mechanisms. Characterization of niches showed that minimum temperatures and aridity are the main climatic variables influencing the abiotic tolerances of these species. Several species close to sugarcane show niche optima in cold climates and are prospective candidates to future research for breeding cold tolerant cultivars. Additionally, we found that most species of sugarcane wild relatives are able to endure a narrow set of climatic conditions with two notable exceptions, *S. spontaneum* and *M. floridulus*, which present a very broad niche. Comparison of niches in environmental space showed that although niches are not identical, it is not possible to support neither hypotheses of niche divergence or conservatism. Finally, we found evidence that selection and neutral processes acted on the evolution of the two dimensions of these species' climatic niche. Thus, using an ecological and evolutionary comparative approach, we were able to decrease the extent of knowledge gaps about the geographical distribution, abiotic tolerances and the evolution of species related to sugarcane, contributing to future conservation of genetic resources and breeding efforts.

Keywords: Sugarcane Crop Wild Relatives; Climatic Niches; Geographical Ranges; Niche Evolution.

1.1 Introduction

Yield projections show that, given current increase rates, food production will not attend the demands of the growing human population (Ray et al., 2013). Also, arable land, already under pressure by degradation and urbanization, will diminish in tropical areas due to climate change (Zabel et al., 2014). Also, an increase in the occurrence of extreme climatic events, such as droughts, heat waves and floods is expected (Cai et al., 2014; Cook et al., 2014). Therefore, in order to promote sustainable increase in food production, crop breeding will have to produce not only more productive varieties but also varieties more resilient to biotic and abiotic stress and with increased input efficiency (Godfray et al., 2010).

Although crop breeding has been extremely successful in increasing productivity of agriculture in the last century, the challenges laid out above demand the advent of new approaches to this scientific field (Wallace et al., 2018). In this regard, it is of paramount importance to explore the diversity stored in crop wild relatives (CWR), as well as landraces and undomesticated wild species, since they can be potential donors of alleles associated with important traits for crops, such as abiotic stress tolerance and disease resistance (McCouch et al., 2013). The domestication process of a crop is normally

characterized by strong selection and genetic bottlenecks - although the frequency and intensity of those demographic processes varies among different species - which leads to reduced genetic diversity within crops as compared to their wild relatives (Meyer e Purugganan, 2013).

Despite their importance, several biological and technical difficulties hinder the use of CWR in plant breeding (e.g., interspecific crossing barriers, linkage drag and difficulties in gene transfer), however, the most important barrier to the use of CWR is the lack of data on these species (taxonomic, genotypic, potential uses) (Dempewolf et al., 2017). In fact, a recent comprehensive study used bioclimatic variables and occurrence records to model the geographical distribution of the 1,076 wild relatives of 81 crops, showed that 72% of the crop gene pools were poorly represented in genebanks and were classified as high priority for collecting. Additionally, 95% of CWR are underrepresented when considered their full geographical range and their ecological variation (Castañeda-Álvarez et al., 2016).

Therefore, information on CWR climatic niches, geographical distribution and the processes and mechanisms underlying their evolution are crucial to their conservation and effective use in crop breeding. Studies of this nature have been done for CWR of some crops, such as: tomato (Nakazato et al., 2010), sunflower (Kantar et al., 2015), strawberry (Johnson et al., 2014), brinjal eggplant (Syfert et al., 2016) and pigeon pea (Khoury et al., 2015). However, there is a significant lack of information about crops of major economic and social importance such as cassava, maize and sugarcane (Castañeda-Álvarez et al., 2016).

Sugarcane is one of the most economically important crops worldwide in terms of tons harvested and planted area (FAOSTAT, 2017). It is also the third plant source of calories in human consumption, only surpassed by rice and wheat (Moore e Botha, 2013). Modern sugarcane cultivars are hybrids from species of the genus *Saccharum* L., that belongs to the tribe Andropogoneae and subtribe Saccharinae, which comprises other genera (Soreng et al., 2017). Besides *Saccharum*, this subtribe also includes the genus *Miscanthus* Andersson, that contains species used as a source of biofuels and cellulose (Brosse et al., 2012) and as ornamental species (Meyer, 2004).

The delimitation of species and genera related to sugarcane has been historically difficult due to the high frequency of natural hybridization events between sympatric species, different modes of chromosomal transmission in these events and high intraspecific chromosome number variation (Amalraj e Balasundaram, 2006). This high frequency of hybridization led to the creation of the concept of the “*Saccharum* Complex”, a group of interbreeding species that were supposed to be involved in the sugarcane origin and included the genera *Saccharum*, *Narenga* Bor, *Sclerostachya* (Andersson ex Hack.) A. Camus and *Erianthus* Michx. (Mukherjee, 1957).

In the literature it is possible to identify two main currents of thought about the systematics of the sugarcane relatives: one understands *latu sensu* (*l. s.*) the genera *Saccharum* and *Miscanthus*, in which the first includes all the species of *Erianthus* and the second includes *Narenga*, *Sclerostachya* and the genus *Miscanthidium* Stapf (Clayton et al., 1986; Kellogg, 2015), an hypothesis that has prevailed; and another, a *stricto sensu* (*s.s.*) view that supports the separation between *Saccharum* and *Erianthus*, restricting the former to the six species highly related to the sugarcane (*Saccharum officinarum* L., *Saccharum spontaneum* L., *Saccharum robustum* E.W.Brandes & Jeswiet ex Grass, *Saccharum barberi* Jeswiet, *Saccharum sinense* Roxb. and *Saccharum edule* Hassk.) and proposes the separation of *Miscanthus*, *Narenga* and *Miscanthidium* (Watson et al., 1992).

Molecular systematics approaches have been recently used in order to address these questions. Hodkinson et al. (2002) showed that *Saccharum l. s.* and *Miscanthus l. s.* were not monophyletic, since species of *Erianthus* from the Old World (section *Ripidium*) should be allocated in a different genus *Tripidium* H. Scholz (under *Ripidium*), and that *Miscanthidium* species were placed outside *Miscanthus*. However, the authors did not find enough evidence to support the separation of *Saccharum l. s.* in *Saccharum s. s.*, *Erianthus* and *Narenga*.

A more complete molecular phylogeny of the tribe Andropogoneae, based on the sequencing of five low copy nuclear genes and considering more species, also supported the polyphyly of *Erianthus* and confirmed the existence of *Tripidium* as a clade separated from *Saccharum* and *Miscanthus* (Welker et al., 2015). They found that the *Erianthus* from the New World form a clade with the *Miscanthidium* (represented by *Miscanthus ecklonii* (Nees) Mabb.), and they are related to the *Saccharum s. s.* (represented by *S. officinarum*). At last, they propose that *Narenga* (under *Saccharum narenga* (Nees ex Steud.) Hack.) is a hybrid between *Saccharum s. s.* and *Miscanthidium*.

Evans et al. (2019) published the most complete molecular phylogeny to date of the Andropogoneae, based on whole chloroplast genome and low copy nuclear genes. The authors confirmed previous evidence that the species from the former *Erianthus* sect. *Ripidium* belong to a different genus, *Tripidium*, distantly related to Saccharinae. They proposed the “core Saccharinae” clade, that comprises: *Miscanthus*, *Miscanthidium*, composed of species that were classified as belonging to *Miscanthus*; New World *Erianthus* and *Saccharum s. s.*

Despite having made the systematics and taxonomy of sugarcane CWR complex, the high frequency of natural hybridization among these species has possibilitated the extensive use of wild relatives in sugarcane breeding. For instance, modern sugarcane cultivars are the result of crosses between *S. officinarum* and *S. spontaneum*, the latter of which was utilized in sugarcane breeding because of its high ratooning capacity and its known adaptation to several environmental stresses (Daniels et al., 1987). It is estimated that approximately 20% of the genome of modern sugarcane cultivars is derived from *S. spontaneum* (Piperidis et al., 2010).

Further attempts to use wild relatives in sugarcane breeding have been recorded, especially using species from the former genus *Erianthus* from the Old World, in detriment of other groups, such as: *Saccharum arundinaceum* Retz. (Piperidis et al., 2010; Ram et al., 2001), *Saccharum longisetum* (currently *Melinis longiseta* (A.Rich.) Zizka) (Cai et al., 2005), and *Saccharum rufipilium* Steud. (Wang et al., 2009). However, studies have shown that crosses between sugarcane hybrids and *S. arundinaceum* results in a small number of true hybrids with aberrant chromosome behaviour (aneuploidy, chromosome loss and duplication, interspecific recombination) (Wu et al., 2014; Huang et al., 2015). The clarification of the phylogenetic relationship may help us understand the difference of effectiveness in using genetic resources from *Saccharum s.s.* and *Tripidium* in sugarcane breeding, since the latter one is evolutionarily distant.

Therefore, the effective use of these genetic resources effectively demands a thorough understanding of the phylogenetic relationships and the evolution of the sugarcane wild relatives to be able to access their potential as trait donors. In this context, although the results from Castañeda-Álvarez et al. (2016) showcase the important gap in our knowledge about sugarcane CWRs, it is necessary to highlight that, from the eleven species analyzed, four belong to the ‘core Saccharinae’ (three subspecies of *S. spontaneum* and *S. robustum*) and the remaining seven species belong to *Tripidium*, which are not considered sugarcane wild relatives in light of the most recent phylogeny of the group.

Hence, given the importance of sugarcane and *Miscanthus* as economically relevant crops and the knowledge gap about the ecology and evolution of their wild relatives, this study aimed to: i) to use Ecological Niche Models (ENMs) to model the potential geographical distribution of wild “core Saccharinae” species; ii) to use ordination techniques to characterize their climatic ecological niches and identify species that are potential trait donors to sugarcane and commercial accessions of *Miscanthus*; iii) to compare the climatic niches of the species under study in search of ecological patterns in the group; iv) to use phylogenetic information in conjunction with the ecological data produced in order to understand the geographical mode of speciation of the group and the evolutionary forces driving the diversification of sugarcane wild relatives climatic niches.

1.2 Conclusions

In this study, we were able to use ENMs to predict the potential geographical distribution of 15 species of sugarcane wild relatives. Additionally, ordination techniques were used to characterize and compare the climatic niches of these species. We found that minimum temperature and aridity are the main climatic variables that influence the ecology of sugarcane wild relatives. Also, most sugarcane wild relatives present their niche optimum in cold climates, meaning that these species are a valuable genetic resource for breeding cold tolerance to commercial cultivars of sugarcane and *Miscanthus*. The range of climatic conditions presented great variation within clades and most species studied are restricted to a narrower set of environmental conditions. Two species (*M. floridulus* and *S. spontaneum*) are climate generalists and are able to occur in broader range of climates. The differences in niche breadth and the arrangement of climatic niches on the environmental space resulted in a pattern of non-identical niches. However, there was not enough evidence to support either niche similarity or divergence.

We used available genetic data to reconstruct a phylogeny of 9 species, from the 15 included in this study. This phylogeny was used to investigate the geographical and ecological aspects of the evolution of this group. We found that closely related species tend to occur in sympatry and that different clades are allopatrically distributed. This pattern resulted in a significant negative correlation between the time of divergence events and sympatry, which suggests that non-allopatry is predominant within this clade. Furthermore, we found evidence for two different macroevolutionary processes having acted on the evolution of niche optima in sugarcane relatives. In relation to temperature, natural selection may underlie the divergence of sugarcane relatives in two ecological groups of species, one adapted to cold climates and the other adapted to warm climates. On the other hand, optima related to aridity seemed to arise under a neutral process.

Finally, we were able to demonstrate the importance of analyzing available biodiversity data in the light of ecological and evolutionary theory. However, even with our results, there is still a knowledge gap about the distribution and the phylogenetic relationships of sugarcane wild relatives, despite their economic relevance. This lack of information hinders the conservation of potential genetic resources to crops and a more complete understanding of ecological mechanisms underlying the diversification of this group.

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