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Explaining the decrease in the genetic diversity of wheat in France over the 20th century

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ABSTRACT

Changing and more volatile climate conditions are leading to higher vulnerability and lower resilience for crop production. Recent studies indicate that crop diversity in agricultural fields may ensure pest control and yield stability in the face of environmental changes. However, few studies have evaluated crop diversity in the field, especially at the within-species level. Applying a new indicator, $H_T{}^*$, which integrates both the spatial evenness of different varieties and molecular genetic data (within and between variety genetic diversity), we followed the evolution of bread wheat genetic diversity on French agricultural landscapes during the 20th century. To our knowledge, the monitoring of crop genetic diversity at such a large but detailed spatial and temporal scale has never before been conducted. In comparison to two frequently used but less integrative indicators (the number of varieties grown in the field and their allelic diversity as measured by the Nei index), the $H_T{}^*$ indicator revealed increasing genetic homogenization overall. This trend was due to the disappearance of diversity within varieties (initial replacement of landraces by more homogeneous old lines and later by modern pure lines), to the spatial homogenization occurring in the last period of the 20th century with the different 'départements' (French administrative territories) progressively cultivating the same varieties and to their increasing genetic similarities. This result calls into question the effects of plant breeding, seed system organization and seed regulation on wheat genetic diversity, especially in the context of current environmental changes.

1. Introduction

During the 20th century, agriculture experienced major gains in productivity via homogenization and intensive use of inputs, but this agricultural system is now jeopardized due to rapid global change, increased environmental stochasticity and the need for greater sustainability of agriculture (see for instance yield stagnation since 1996 in Brisson et al., 2010). Crop diversity in the field (between and within species) has been identified as a key factor for crop resilience in the face of global change, to buffer more variable environmental pressures, drought and the emergence of new diseases (Zhu et al., 2000; De Vallavieille-Pope, 2004; Ostergard et al., 2009; Huang et al., 2012; Mulumba et al., 2012). Beyond agricultural production issues, crop diversity has recently been shown to be instrumental in maintaining other ecosystem services such as wild biodiversity associated to agro-ecosystems (Wimp et al., 2004; Hajjar et al., 2008; Bailey et al., 2009; Chateil et al., 2013). Assessing *in situ* crop genetic diversity over time is thus critical for the evaluation of potential threats on agroecosystems and the consequences of the past changes in agricultural practices.

The available genetic diversity of crops in collections or in the catalogues of registered varieties at different points in time has been evaluated in many studies (*e.g.*, Roussel et al., 2005; Le Clerc et al., 2006; Chao et al., 2007; Spataro et al., 2011; Courtois et al., 2012; Borner et al., 2012). There is however a lack of information on in-field crop diversity, especially at the within-species level. *Ex situ* conservation is used mainly by breeders to maintain reserves of seeds stored at low temperature. Conservation at low temperature requires regular regeneration of the seed samples (*i.e.*, growing plants from each seed sample to harvest new fresh seeds). This practice is often carried out far from the original environment and

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over several generations, raising the question of the adaptability of such genetic resources (Diederichsen and Raney 2008; Soengas et al., 2009; Jensen et al., 2012). This question is especially important when considering the necessity of providing varieties that are less dependent on chemical use and might be plastic enough to adapt to climate change. Assessing crop genetic diversity in the field would shed light on how genetic resources are used to create new varieties in breeding programs.

Monitoring biodiversity in general and crop genetic diversity in particular, requires robust indicators agreed upon at the international level. The number of different entities, their frequency in a given territory and the extent of differences between them are facets to be considered in the design of biodiversity indicators (CDB SBSTTA 10, 2005). Moreover, the temporal and spatial scales chosen to carry out this monitoring should be adjusted according to the objectives (Dumbrell et al., 2008; Dengler, 2009). Indeed, due to homogenization between sites, diversity may remain large at a local scale while decreasing at a larger scale (Smart et al., 2006; Kallimanis et al., 2008). Monitoring diversity during too short a period may also lead to misinterpretation about the level of threat for the species or ecosystem studied (Duffy, 2011).

Hence, identifying changes in crop diversity in order to link them to important changes in agricultural practices of the 20th century requires both appropriate indicators and the use of relevant temporal and spatial scales to detect trends and analyse their origins. Bonneuil et al. (2012) developed a new indicator for crop diversity assessment, H_T^*, which combines spatial distribution data (variety spatial evenness) with information at the level of molecular data (within- and between-variety genetic diversity) and have compared it with less integrative pre-existing indicators.

In this study we undertook to use this new indicator to follow the evolution of bread wheat genetic diversity in agricultural landscapes over one century and over the whole French territory. In 2012, France, with five million hectare (34% of the crop area according to the French Ministry of Agriculture http://agreste.agriculture.gouv.fr/), was the leading European wheat producer and the fifth producer at the world level. French wheat production thus makes a significant contribution to the global state of the *in situ* genetic diversity of wheat. Our results, analyzed in light of the evolution in plant breeding and varietal regulation in France, show a strong reduction of *in situ* genetic diversity over the last century. This genetic homogenization appears to be due to the disappearance of diversity within varieties, increasing genetic similarity among varieties, and spatial homogenization with diverse French regions ('départements') progressively cultivating the same varieties. This homogenization raises the issue of the sensitivity of wheat crops with respect to current and future environmental changes (pathogens, drought, sustainable agricultural practices, *etc.*).

2. Materials and methods

2.1. An integrative crop diversity indicator

Until recently, crop diversity indicators were limited and poorly integrative (SEBI, 2010). They consisted mostly of (a) numbers of varieties conserved in *ex situ* gene banks or grown in agricultural landscape accounting for variety richness, (b) acreage shares of the five top varieties providing an insight for evenness (OECD, 2001), and (c) the Nei index (Nei, 1973), accounting for allelic diversity among varieties conserved in gene banks (for a survey of 162 studies on crop diversity, see Goffaux et al., 2011 and Supplementary materials). A new and more comprehensive indicator, H_T^*, has been proposed by Bonneuil et al. (2012) which works at the scale of a given geographic area. This integrative indicator of crop genetic diversity accounts for (i) varietal richness in the area, (ii) varietal evenness of spatial distribution in the area, (iii) between-variety allelic diversity, and (iv) within-variety allelic diversity. The first three components were included in an intermediate parameter (H^*) based on a formula derived from Nei's gene diversity (Nei, 1973) where allele frequencies were estimated at the spatial scale (weighted allelic frequencies, p^*) (Bonneuil et al., 2012):

$$H* = \sum_j \frac{\left(1 - \Sigma_i \, p*_{ij}^2\right)}{J}$$

with i the allele index and j the locus index varying from 1 to J the total number of loci. While H^* reflects the whole of the *in situ* diversity when pure lines (genetically homogeneous) are grown in the fields, it does not account for the within-variety diversity component (iv) in the more general case. Indeed, the history of plant breeding and seed regulation reveals three groups of varieties according to their level of homogeneity: (1) landraces and varieties derived from mass selection, (2) "old" commercial lines which hold some within-variety allelic variability (in France corresponding to inbred lines derived by pedigree selection from artificial crosses, after 1884 and before 1945), (3) modern pure lines with zero within-variety allelic diversity (in France, these correspond to cultivars registered from 1945 onwards) (Bonneuil et al., 2012; Bonneuil and Thomas, 2010).

H_T^* further includes the within-variety diversity component (iv) as follows:

$$H_T* = \frac{H*}{G_{ST}}$$

with G_{ST} the between-variety genetic differentiation relative to the total genetic diversity (see Bonneuil et al., 2012 for more details on the approach and Nei, 1973, for the theoretical bases). Given that assessing within-variety genetic diversity was not possible for all the varieties and for each year/generation, the contribution of within-variety diversity to the total genetic diversity (through the G_{ST} parameter) included in the calculation of H_T^* was estimated globally for each of the three groups of French varieties. From an extensive survey of the bibliography and after sensitivity tests (see Bonneuil et al., 2012) the G_{ST} coefficient was set: (1) to 0.4 for "landraces", which is a rather conservative level as compared to the range of values documented in the literature for wheat or barley landraces (G_{ST} = 0.19–0.48, average: 0.35); (2) to 0.94 for "old commercial lines" corresponding to a within-variety diversity of around 10% of the landraces; (3) to 1 for "modern lines" corresponding to a null value for their within-variety diversity.

Changes in crop diversity in a territory were thus assessed using the integrative indicator H_T^* in contrast to the two frequently used but less integrative indicators: the number of varieties grown in the territory and the Nei diversity index (Nei, 1973) accounting for genetic diversity among varieties.

2.2. Historical data on spatial distribution

As our objective was to assess changes in crop diversity and to link them to important changes in agricultural practices of the 20th century, and assuming that different territories in France might have been shaped by different histories, we looked for a scale finer than the national level. Metropolitan France is subdivided into 90 administrative districts, the 'départements'. Agricultural professional societies and services are organized in each 'département'. Hence, throughout the past century cultivar acreage data has been reported for some years at both this regional level and the national level, with the regional level naturally providing finer grain spatial information on cultivar distribution than the national level. Statistical services of the Wheat Board and/or of the Ministry of Agriculture started systematic surveys from the 1960s on