



Temporal evolution of varietal, spatial and genetic diversity of bread wheat between 1980 and 2006 strongly depends upon agricultural regions in France



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ABSTRACT

An in-depth analysis of the spatio-temporal evolution of crop diversity in agricultural landscapes is necessary to provide insights on how to improve the resilience of agroecosystems to climate instability and new pest pressures by increasing *in situ* crop diversity, while promoting a greater sustainability of agriculture. However, most of the indicators of crop diversity used in previous studies were based on *ex situ* genetic diversity, or on official lists of varieties or breeding programs, without taking acreage of the varieties actually grown in farmers' fields into account. Acreage of varieties represent however a relevant information to assess the actual genetic vulnerability of a crop (genetic uniformity at landscape scale) cultivated in the considered regions over the period studied. To bridge this gap, we analyzed spatial varietal and genetic diversity of bread wheat in France – an important production area – over the 1980–2006 period at a yearly time step and a district scale, i.e. 'département'. We used H_T^* , an indicator integrating both the spatial evenness of variety distribution and molecular genetic data, to finely examine the spatio-temporal evolution of spatially weighted bread wheat genetic diversity. We also computed several simpler and complementary indicators accounting for the number of varieties, the spatial varietal diversity and the genetic diversity, and we estimated the individual contribution of these simpler indicators to the spatio-temporal structure of the spatial genetic diversity H_T^* . H_T^* values showed significant but non linear temporal evolutions between 1980 and 2006, these evolutions being besides spatially structured. Moreover, both spatial varietal diversity and genetic diversity partly explained these temporal changes of H_T^* values while the number of varieties appeared non-explanatory. Similarly to H_T^* , all indicators studied also showed substantial differences of temporal changes among major French agricultural regions, furthermore sometimes opposite for varietal and genetic diversity. As an example, in the north of France, varietal richness and spatial varietal diversity showed a substantial increase, suggesting the adoption of an increasing number of bread wheat varieties by farmers in this region. However, considering that genetic diversity showed a slight but continuous decrease over the recent period, this could suggest an increase in genetic similarity among bread wheat varieties chosen by farmers. Taken as a whole, our results suggest that several determinants of crop diversity, such as the shortening of crop sequences or the recurrence of epidemics of some pathogens, could differentially affect varietal choices of farmers and thus the spatial structuration of the temporal changes of crop diversity. Finally, our results question the dominant use of *ex situ* nationwide datasets to characterize the evolution of spatial genetic diversity as a proxy of genetic vulnerability of a crop to face with future changes.

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1. Introduction

Maintaining *in situ* crop diversity is regarded as one relevant way to ensure the resilience of agroecosystems to climate

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instability and new pest pressures, while promoting a greater sustainability of agriculture (Costanzo and Bàrberi, 2014; Østergård et al., 2009). For instance, enhancing intra-crop diversity within a field allows a greater yield stability, especially by buffering the influence of pest pressures due to diversifying disease resistance genes (de Vallavieille-Pope, 2004), while a lack of intra-crop diversity can lead to devastating epidemics (Ullstrup, 1972). Disease resistance may also be managed at the landscape scale because pathotype frequencies on particular varieties are known to be affected by the landscape varietal composition (Papaix et al., 2011). Both inter- and intra-crop diversity may also deliver ecosystem services in addition to production, such as promoting wild biodiversity associated to agroecosystems, e.g. pollinators and predatory carabids (Chateil et al., 2013; Gaba et al., 2015; Hajjar et al., 2008).

On the twentieth century, characterized by the improvement of modern agricultural practices and scientific breeding methods, two major periods of genetic erosion have been identified. The first period was related to the replacement of landraces by modern pure lines, while the second period was related to the widespread use of key genes adapted to modern agricultural practices associated with the diffusion of a reduced number of high yielding semi-dwarf varieties (see van de Wouw et al., 2009 for details). In France, a previous study highlighted these periods over the twentieth century at a national scale (Bonnin et al., 2014). First, Bonnin et al. (2014) confirm a gradual process of genetic erosion during the first half of the twentieth century when landraces were replaced by modern pure lines due to the use of a limited number of landraces as parents of new cultivars and the registration of only genetically fixed and homogeneous varieties since 1945 in France (Bonneuil and Thomas, 2009). Then, they identify a strong genetic homogenization between 1965 and 1970 due to the increasing percentage of acreage of a few successive leading varieties over large geographical areas of the French territory after the Second World War, in accordance with other studies in European countries (e.g. White et al., 2008).

In this context, our study has focused on the last quarter of the twentieth century when the landscape varietal composition was dominated by modern pure line semi-dwarf varieties, i.e. we did not consider these two previous periods of strong genetic erosion. For the last quarter of the twentieth century, we assessed, at a fine spatio-temporal scale, *in situ* genetic diversity of bread wheat, which is more closely related to genetic vulnerability of the crop faced with future changes. Given our knowledge of the temporal evolution of crop diversity over the whole twentieth century (Bonnin et al., 2014), our study focused on France, a country characterized by bread wheat acreages between 4.3 and 5.0 million hectares per year over the period 1980–2006. This country includes several major contrasting bread wheat production areas characterized by different pedoclimatic conditions, cropping systems and end-use markets, thus representing a relevant case study to finely examine a potential spatio-temporal structuration of crop diversity. Moreover, in contrast with many studies characterizing *ex situ* genetic diversity trends over the twentieth century based on official lists of varieties (see van de Wouw et al., 2010 for a review), our aim was to measure *in situ* genetic diversity trends within agricultural landscapes during a recent period. Under these conditions, we used an integrative indicator H_T^* which has been recently proposed to assess spatial genetic diversity while taking into account varietal, spatial and genetic diversity at a landscape scale (Bonneuil et al., 2012). However, because of its integrative nature, the interpretation of spatio-temporal trends of H_T^* may be difficult as several determinants of crop diversity influence differently the varietal richness, the spatial evenness of distribution of varieties and the genetic diversity. For instance, while some determinants might have promoted varietal diversity,

e.g. the increase in the number of varieties available (Silhol, 2010), others might have reduced genetic diversity, e.g. the selection method generating new elite varieties by intermating the best varieties of the previous breeding cycle. Therefore, for a better understanding of H_T^* trends, it seems useful to perform a joint analysis using a set of simpler complementary indicators characterizing separately the varietal richness, the spatial evenness of variety distribution and the genetic diversity.

In this study, we were thus interested in varietal richness, spatial diversity and genetic diversity of bread wheat in France, focusing on a recent period, i.e. 1980–2006, and at the scale of a limited geographical area defined administratively, i.e. the district level (thereafter ‘département’), in order to finely examine the spatio-temporal evolution of bread wheat diversity, previously known to have decreased back to the values of the 1960s at national scale (Bonnin et al., 2014). We addressed the following questions:

- (1) How does the spatial genetic diversity of wheat, here summarized by the integrative indicator H_T^* , change over the 1980–2006 period at the ‘département’ scale? In particular, is the diversity stable over the period or are there any significant trends?
- (2) To what extent and in what ways are the changes of H_T^* over the 1980–2006 period at the ‘département’ scale determined by simpler diversity indicators (varietal richness, spatial diversity and genetic diversity)?
- (3) Is the crop diversity level and its temporal evolution spatially structured in bread wheat? If so, is this spatially structured pattern comparable between H_T^* and the different indicators?

2. Materials and methods

2.1. Data sources

The dataset was described in details by Bonneuil et al. (2012) and Bonnin et al. (2014) and includes data on the allelic diversity of 1102 varieties, the acreage of each variety for each ‘département × year’ particular combination over the period 1980–2006, and the category of each variety, i.e. either landraces, old commercial lines or modern pure lines, similar to Bonnin et al. (2014).

Molecular data consisted of genotypes at 35 microsatellite markers, mainly highly polymorphic and distributed across the whole genome, previously used to characterize genetic diversity, e.g. in Roussel et al. (2004, 2005). For details on microsatellite markers and genotyping procedure, see Bonneuil et al. (2012).

Acreage of each variety are based on systematic surveys of the Wheat Board (i.e. Office National Interprofessionnel des Grandes Cultures then FranceAgriMer) over the period 1980–2006 in 70 of the French ‘départements’ at a yearly rate following a similar procedure over the whole period. A questionnaire was sent to around 500 farmers in each ‘département’, representing between 2000 and 3000 wheat fields per ‘département’. For each field, both the acreage and the variety chosen were given (mainly sown in pure stand; an extremely small percentage of wheat variety mixtures has been reported by surveyed farmers over the period). Sampling effort can be considered relatively comparable among ‘départements’. However, total bread wheat area can be low in some ‘départements’, especially in the south-east. Several ‘départements’ were not surveyed every years leading to missing data. Overall 1023 varieties were documented between 1980 and 2006, among which 710 have been genotyped.

To quantify the genetic diversity, we considered both between- and within-variety allelic diversity due to the occurrence of a low percentage of landraces and old commercial lines, i.e. less than 2%

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