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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 agroecosystems (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 'départements'. 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 documenting the acreage and share of wheat varieties in most of the French 'départements' at an almost yearly rate. In addition to this readily available data, we found other data scattered through published or unpublished agricultural monographies, journals of local learned societies, and archives of 'départements'. For the early 1950s, we could refer to quantified data from 1950 monographies conserved in the Wheat Board's archives and from the 'Monographies départementales agricoles' launched in 1952. For the interwar years, we found relevant data in national cultivar surveys, 'départements' agricultural monographies, and journals of local agricultural societies.

For 1912, a published nation-wide study on the distribution of wheat varieties (Brétignière, 1912) provided quantitative data in 65 'départements' on the distribution of circa 30 varieties. Still, Brétignière estimated the total number of bread wheat cultivars grown in France to "more than 100 varieties" while the 1933 wheat register ("Catalogue des Espèces et Variétés cultivées en France", 1933) documented circa 400 cultivars. Out of these 400, we identified circa 140 varieties that existed already in 1912 suggesting that more than 140 were grown in France during this period. From these 140, an intensive survey of additional historical sources around 1912 at both the national (Garola, 1909) and the 'départements' levels (articles in journals of local agricultural societies, local archives, *etc.*) made it possible to obtain acreage data for 57 cultivars in the 65 'départements'. Thanks to these combined sources, we could reconstitute a valuable picture of 1912. Still, as we always took the most cautious decision as to the presence and acreage of a variety, the value of all indicators for 1912 should be considered as a minimum value rather than the best approximation.

Overall 1314 varieties were documented between 1912 and 2006. Acreage for each cultivar was usually provided at the 'département' scale, thus affording variety distribution at the national scale (knowing the wheat acreage of all 'départements'). For the period 1926–1937, 'département' scale data were insufficiently available to carry out calculation at the national scale. Distributions given at the national scale by literature sources were thus used directly. We however confirmed that when both types of scale were well documented between 1985 and 2006, similar values of $H_T{}^*$ were found at the national scale. Analyses of the literature showed that less frequent varieties before the 1980s were under-recorded whatever the source, leading to underestimation of all indicators (Bonneuil et al., 2012). Conversely, data from the last 30 years were more accurate and cultivars found in less than 0.01% of departmental wheat area were even considered.

2.3. Molecular data

A set of 35 microsatellite markers evenly distributed along the wheat genome was developed by the Genotyping Platform at INRA Clermont-Ferrand. They were used to describe the allelic compositions of 1104 varieties (from among the 1314 documented) that could be obtained from either European wheat genebanks or from seed companies. Data for 816 of these 1104 varieties were produced by Roussel et al. (2004, 2005), while data for the remaining 288 were obtained in 2009 for this study.

2.4. Data treatment and statistical analyses

To calculate the $H_T{}^*$ indicator, it was necessary to estimate the proportion of each cultivar grown each year in the total wheat area of each studied 'département' and to use molecular markers to obtain genotypic data for all cultivars. Both types of information were entered into a database. Functions were developed that make it possible to automatically compute the number of varieties, Nei genetic index (H) and $H_T{}^*$ for each year in each 'département'. For each indicator, we compared (1) values obtained at the national level, and (2) average values obtained at the 'département' level weighted by wheat acreage of each 'department' each year. If (1) and (2) were of similar levels, it meant that the whole of the diversity could be found within each 'département', and that 'départements' were quite similar in their composition. On the contrary, if (1) appeared much higher than (2), it meant that 'départements' were less diverse than the whole but that they were quite different from each other. Ideally, the alpha, beta, gamma diversities (Whittaker, 1972) for multiple communities should be applied using 'départements' as communities but the hypotheses underlying the theory were not met here (Jost, 2006), nor were the data required to assess the alpha, beta, gamma parameters available. Hence, as a proxy for among 'départements' contribution to overall diversity, we computed the difference between $H_T{}^*$ at the national level and the weighted average of $H_T{}^*$ at the 'départements' level.

For each 'département' and each year, $H_T{}^*$ was calculated only (i) when at least 70 % of wheat acreage could be attributed to genetically characterized cultivars (see Goffaux et al., 2011; Bonneuil et al., 2012); (ii) using loci with a minimal frequency of genetic data above 0.95; (iii) and when genetic data were obtained from at least 15 of the 35 loci. The accuracy of the $H_T{}^*$ estimates results from a compromise between the level of information provided by each locus and the number of loci used for estimation. Setting the threshold for genetic data frequency at each locus at a very high level (0.95) meant that only those loci with very little missing data were retained, thus providing an accurate estimation of allele frequency but that might be based on fewer loci (a minimum of 15). Bonneuil et al. (2012), (Suppl. Fig. 1) found that this had little impact on $H_T{}^*$ values. Indeed, although increasing the number of loci would increase the accuracy of diversity estimates, a minimum value of 15 loci seemed reasonable as even very recent studies used 8–15 microsatellite loci to analyze genetic diversity within and among populations (e.g., Marchi et al., 2013; Nazareno et al., 2013; Ye et al., 2014).

'Départements' that might have undergone an evolution of similar agricultural practices are expected to show similar evolution of diversity. In order to reveal regional trends in the diversity of their evolution we used a multivariate analysis, DAPC (discriminant analysis of principal components in Jombart et al., 2010). With this analysis we identified clusters of 'départements' showing the same range of $H_T{}^*$ variations. The principle is to consider all annual $H_T{}^*$ values for all 'départements' as multitrait data. Because multivariate analyses do not allow for missing data, we had to extract the largest and most complete dataset from the whole database. First, years with missing datasets (*i.e.*, with less than 45 'départements' documented) were either discarded or when possible, grouped with one or more preceding or following years. The result was at least 50 'départements' for each of the 20 periods studied (except for 1959–1971 where 46 'départements' were analyzed). Then, 'départements' described for less than 15 periods were discarded. Finally, we obtained a set of 57 'départements' × 20 time periods where only a minimum number of individual data were still missing (less than 5%). They were replaced by the average value over all 'départements', which is the classical conservative approach (differences between 'départements' were not over-estimated by so doing). The mean value was also used when several departmental values of $H_T{}^*$ were available at one period.

The first step of this analysis consisted in applying a principal component analysis (PCA) on $H_T{}^*$ departmental values to get new non-correlated variables (axes) explaining the whole variation. In a second step, K-means clustering of principal components (Liu and Zhao, 2006; Lee et al., 2009) was applied to identify groups of 'départements' with similar $H_T{}^*$ evolutions. The principle of

K-means is that it partitions genetic variation into a between-group and a within-group component, and attempts to find groups that minimize the latter. K-means was run with a number of clusters ranging from 1 to 20 and the Bayesian information criterion was used to assess the optimal number of clusters (Jombart et al., 2010). DAPC was performed using the adegenet package (Jombart, 2008) for the R software.

3. Results

3.1. Data set description

A minimum number of 23 loci (in 1990, 2004 and 2005) and 15 loci (in 2004 for one 'département') out of 35 were used to calculate $H_T{}^*$ at the national (Table S1) and departmental scales respectively. Our study documented a total of 1104 varieties sampled for 64 years at a maximum during the period 1912–2006 in 80 'départements'. This amounts to 1312 year × 'départements' $H_T{}^*$ data points. Most data were available for the 'départements' with the largest wheat acreage (northern France and Paris Basin) (Table S2). In 1912, the 55 documented 'départements' represented 73.5% of the country's wheat acreage. In 2006, the 65 documented 'départements' represented 90.7% of the country's wheat acreage (4 810 400 ha out of 4 941 237 ha). Depending on the date, the number of sampled 'départements' varied but in only 19 out of 64 years, mostly between 1924 and 1949, were less than 10 'départements' described (Table S2). The highest number of sampled 'départements' (>55) was observed for 1912 and for the last 20 years. Only 24 out of 80 'départements' were described for less than 15 dates (Table S2). To our knowledge, no such long term, detailed data have ever before been collected in any country for any crop.

3.2. Wheat genetic diversity at the national scale

3.2.1. Number of varieties (variety richness index)

While we were able to document distribution data for no more than 57 cultivars in 1912 due to lack of reporting at the varietal level in historical sources (Fig. 1), other historical documents indicated that they might have been much more (*e.g.*, the 1933 national wheat variety register listed around 400 cultivars). Based on these sources, we estimated that at least 140 varieties were grown in France in 1912 (Fig. 1). The 1960–1970s saw a low water mark with overall only 23 cultivars cultivated in 1964 and 13 in 1974, and a cumulated frequency of the first 5 varieties around 80% at the national scale (Fig. 2). The number of grown cultivars then increased again to almost 400 by the beginning of the 21st century, together with a decrease in cumulated frequency of the first 5 varieties around 40% (Fig. 2).

3.2.2. Nei index (allelic diversity among varieties)

The Nei index remained quite stable from 1912 to the early 1950s (around 0.65). It then fell to around 0.50 in the 1960–1970s, increased back to almost 0.65 by 1990, and finally slightly declined to about 0.6 in 2006 (Fig. 1).

3.2.3. The $H_T{}^*$ indicator (integrative indicator)

When combining both spatial and genetic (including intra-varietal diversity) data as in $H_T{}^*$, diversity showed a strong decline from 1912 ($H_T{}^* = 0.96$; this should be considered as a very minimal estimate given the weakness of data and the conservative judgments made) to the 1960s (reaching a low value of 0.48 in 1968), followed by a slight increase from the mid 1960s to the early 1980s, then a slight decrease from the late 1980s to the end of the studied period (down to 0.48 again in 2004) (Fig. 1). Overall, the results from this most integrative indicator indicate a minimum loss of bread wheat in-field genetic diversity of 50% in France in the last 100 years.

3.3. A regional view

3.3.1. Trends at the 'département' scale and contribution of 'départements' to overall diversity

As at the national scale, only a few cultivars were reported in each 'département' in 1912 due to insufficiently detailed survey methods. The dramatic increase in the number of cultivars grown in each 'département' from around 10 (4–13) in the 1970s to around 50 (6–84) in the 2000s was well documented. During the last 4 decades, decreasing differences between departmental and national values of the Nei index indicated that the among 'départements' diversity decreased, because the same cultivars or genetically related cultivars came to be grown nation-wide. Likewise, for $H_T{}^*$, the variation among 'départements' was larger before the 1960s than after. The estimated difference between the mean value of 'départements' $H_T{}^*$ (weighted by wheat acreage) and the national value, showed a decreasing trend from 1912 to 2006 (0.26, 0.18, 0.11, 0.09, 0.07, 0.06 and 0.03 for 1912, 1952, 1971, 1976, 1986, 1995 and 2006 respectively) indicating that 'départements' increasingly supported more of the same diversity.

3.3.2. Regional pattern of historical evolution of wheat genetic diversity as revealed by $H_T{}^*$

Groups of 'départements' showing contrasting patterns of wheat genetic diversity trends over the 20th century were identified using a DAPC approach (Jombart et al., 2010). PCA was initially performed using a dataset with no missing data, including $H_T{}^*$ values for 57 'départements' grouped within 20 time periods (Table S3). The first four PCA axes represented 60.2% of the total variation. The first axis was related to $H_T{}^*$ in 1912, the second was related to $H_T{}^*$ in the periods 1983–1985 and 2000, the third to $H_T{}^*$ in 1972–1982 and the fourth to $H_T{}^*$ in 1986–1987 and 2003. Seven clusters was the number of 'départements' clusters giving the lowest associated Bayesian information criterion (BIC) (Fig. S1). Evolution of $H_T{}^*$ in the seven groups and their localizations are shown in Fig. 3. Along the period considered, $H_T{}^*$ decreased only slightly for groups 1, 2 and 3, indicating that northern, western and central France had already been characterized by lower levels of diversity in 1912 than other regions, while groups 4–7 showed a higher decrease in $H_T{}^*$ over the surveyed period.

4. Discussion

In a 2011 review of 162 studies assessing bread wheat diversity, Goffaux et al. (2011) identified 20 diversity studies that considered both wheat acreage and at least three temporal samplings since the 60s over a country (list at http://www.fondationbiodiversite.fr/images/stories/telechargement/Annexes_en_ligne_.pdf). No studies, however, integrated both genetic and spatial data/information into the same indicator, weighting genetic diversity of varieties by their frequency in the agricultural landscape. In Europe (Srinivasan et al., 2003; Donini et al., 2000; Roussel et al., 2005; White et al., 2008; Christiansen et al., 2002), the diversity was often estimated maximal in the 40s or earlier when data were available and minimal in the 60–80s. This was also observed in Canada (Fu et al., 2005, 2006; Fu and Somers, 2009) with minimal values after the 80s, while it was the reverse in the USA (White et al., 2008) and in the USSR region (Martynov et al., 2006). In China, India and Australia (Hao et al., 2006; Tian et al., 2005; Ram et al., 2005), diversity decreased from the 50s or 70s until 1990 or 2000. Yet, out of these 20 studies, only four have considered landraces and these did not take within-cultivar diversity into account (Roussel et al., 2004; Reif et al., 2005; Tian et al., 2005; Martynov et al., 2006). The

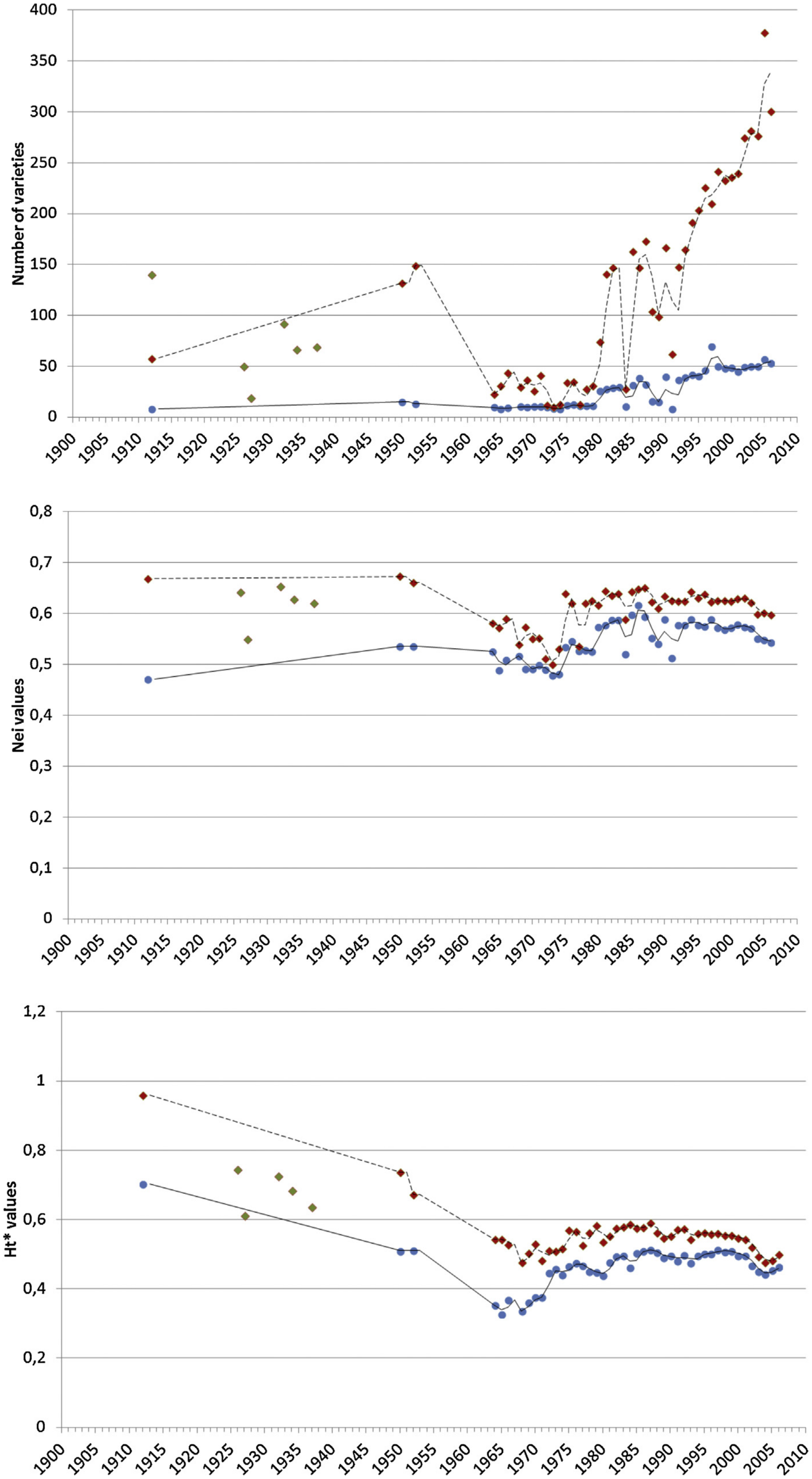

Fig. 1. Evolution of national (diamond) and 'département' (circles) mean values of the number of varieties, the Nei index and the H_T* indicator. Dark and light diamonds were used for national values obtained from recalculation and literature sources respectively. For 1912, two national values were drawn, one (dark diamond) derived from the recalculation of 'départements' data corresponding to varieties with acreage information and the other (light diamond) for an estimation from literature sources where varieties' acreage was not available (see text). The 'départements' mean value correspond to the average over all 'départements' values weighted by the respective 'département' wheat acreage.

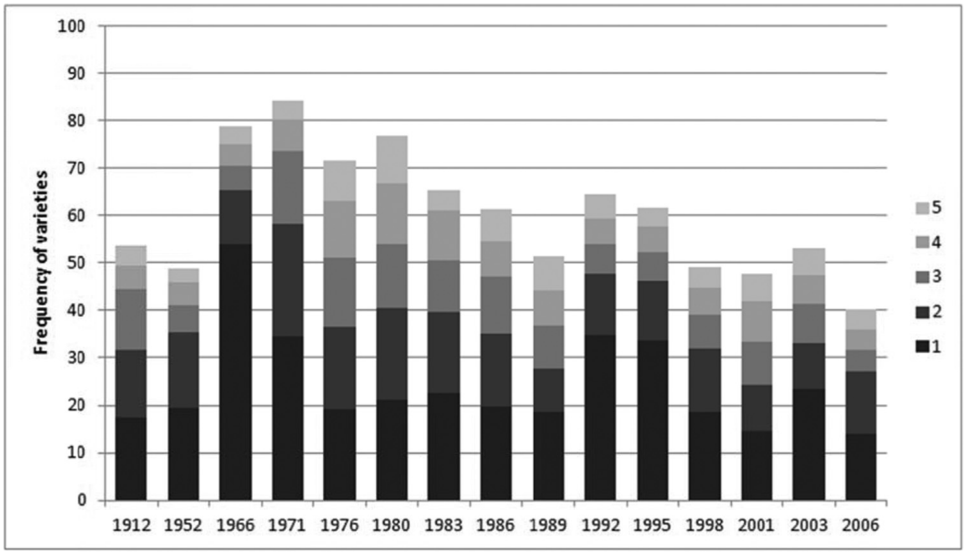

Fig. 2. Cumulated frequency of the first five varieties at the national scale (varieties are numbered from 1 to 5). Frequencies were calculated from available data.

studies in question showed a decrease in genetic diversity, explained by extensive use of a few genitors during the development of modern plant breeding in the studied countries. Here, using a more integrative indicator allowed to confirm this trend but also to analyze in details more complex changes in time and space.

Two issues were encountered during this study: (i) the within variety genetic diversity of landraces, old lines and modern varieties could not be estimated based on real data and we had to make assumptions for their estimation and (ii) the oldest data were less complete than recent. As it has been shown that the assumptions we made were rather conservative (Bonneuil et al., 2012), (i) and (ii) led to the fact that we most likely underestimated the decrease in *in situ* genetic diversity during the first half of the 20th century.

4.1. A long trend of erosion (since 1912)

As revealed by our study, the evolution of wheat genetic diversity on French landscapes can be characterized by three periods with contrasted evolutions of the three indicators:

1) In the first period, from 1912 to circa 1970, unlike the number of varieties, the $H_T{}^*$ index decreased continuously, while the Nei index decreased only after 1950.
2) During the second period, from circa 1970 to the late 1980s, genetic diversity (as shown by the Nei index and $H_T{}^*$) increased slightly without going back to its 1912 initial state.
3) The last period, from circa 1990 to 2006, was marked by a plateau followed by a slight decrease for genetic diversity (as shown by the Nei index and $H_T{}^*$) and a continuous increase in the number of varieties.

These periods can be interpreted in light of the history of the evolution of plant breeding and varietal regulation in France (Bonneuil and Thomas, 2009; Bonneuil and Thomas, 2010).

4.1.1. Fist period: 1912 – circa 1970

In the second half of the 19th century, French wheat landscapes (about 6 million ha) were dominated by local landraces, or by landraces or cultivars imported from Ukraine or England that had been locally adapted. All were managed on-farm, and these varieties underwent evolution through mass selection, mutation, drift and seed exchange. They were genetically heterogeneous; plants of the same variety had similar phenotypic characteristics (Hailu et al., 2010; Serpolay et al., 2011) but different alleles. In the 20th century, a new approach to breeding appeared with industrialization. As milling became more mechanized and centralized and as new agricultural practices were adopted, cultivars that were less prone to "lodging" and were more homogeneous were required. These changes were crystallized in 1884, when the Vilmorin Company released the first French pure line obtained from a self-fertilized progeny of a controlled cross-breeding. From the end of the 19th century to the 1950s, landraces were progressively replaced by lines developed with pedigree selection (at the national level, they were respectively 57.2% and 42.8% in 1912 *vs* 8% and 90% in 1950). These lines here called "old lines" were obtained by 5–10 years of self-fertilization and were genetically far more homogeneous than landraces. A new period of plant breeding and seed regulation started at the end of the Second World War. National authorization was required before a variety could be commercialized. Tests of "Distinction, Uniformity and Stability" (DUS) became increasingly strict. These post WWII cultivars, which are referred to as "modern pure lines" in this study, were more homogeneous than "old lines" and quickly became the major (mainly grown) varieties: they represented respectively 13.2% of the cultivated varieties in 1952 and 100% in 1972.

To conclude, the loss of wheat genetic diversity on French landscapes from 1912 to 1970 is not wholly due to a declining number of varieties available to farmers. Three explanatory hypotheses can instead be posited:

i) A sharp decrease of the within-variety component of genetic diversity, due to the extinction of landraces and to the replacement of old lines by more homogeneous modern lines that had to go through a stringent 'distinction, uniformity and stability' criteria.
ii) A decrease in the number of varieties and the among-varieties component (as indicated by the post-WWII decrease of the Nei index). During this period, only a few old French varieties were used in breeding schemes for crossing with a limited number of new lines introduced from Asian germplasm (Roussel et al., 2004).
iii) A decrease in the evenness component, due to the increasing scale of growing of a few "blockbuster" cultivars (for example Etoile de Choisy, Capelle, Capitole) over large geographical regions of France after WWII.

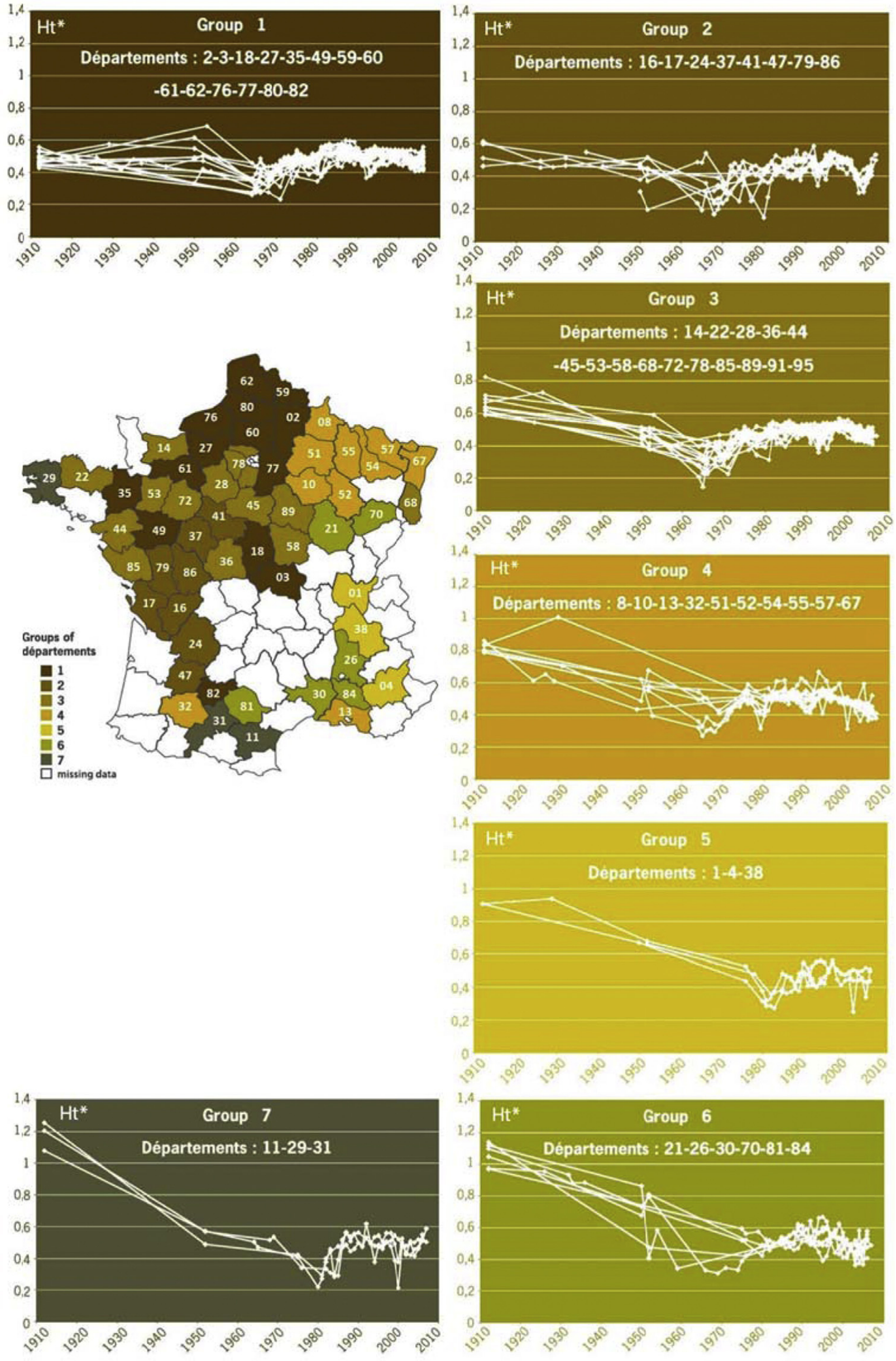

Fig. 3. Groups of 'départements' obtained from DAPC analysis on $H_T{}^*$ values. The color gradient indicates the place of agriculture modernization: from the earliest brown to the latest green. The 'départements' (in white) with less than 15 available temporal periods out of 20 were not considered into the analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

These trends were in line with the "Green Revolution" paradigm for modernizing agriculture after World War II, which was based on industrial norms of efficiency that valued maximal output through a clear homogenization and simplification of crop genetic composition under stable high-input conditions (Bonneuil and Thomas, 2009). This trend might not be specific to France and a somewhat similar pattern is expected in other European countries following the enforcement of the Council Directive 66/402/EEC of 14 June 1966 that limited the marketing of cereal seeds to certified seeds which were sufficiently uniform and stable (http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31966L0402:EN:NOT). This is consistent with trends observed for diversity in UK between the 30s and the 70s (Donini et al., 2000; Srinivasan et al., 2003).

4.1.2. Second period: circa 1970 – circa 1988

During the second period, from circa 1970 to the late 1980s, wheat genetic diversity increased without going back to its highest value from 1912. This is due to the rise in the number of registered cultivars and the larger among-cultivar genetic distance (cf. the increase of the Nei index in this period). It can also be related to a shift in seed policies and in the seed market during this period. With European harmonization of the seed market and France becoming a large wheat exporter, the French registration standard stopped requiring high backing quality for all cultivars. In the early 1970s, the regulatory one-size-fits-all of the preceding period was revised: different kinds of cultivars could be registered for different wheat qualities and uses (bread quality wheat, feed wheat, biscuit wheat, *etc.*). This relaxation in regulations facilitated more diversified breeding strategies. For instance, highly productive English feed wheat cultivars were introduced in the seed market and in breeding programs, providing input from a new genetic background.

4.1.3. Third period: circa 1988 – 2006

During this last period the level of cultivated wheat genetic diversity stagnated and decreased back to the values of the 1960s. This is due to:

i) A decrease in the among-varieties component. It is interesting to note that this decrease in the Nei and H_T* indexes happened while the number of varieties was increasing. A comparative study of the number of varieties and the Nei index suggests that despite the development and release of numerous new cultivars, these cultivars remained closely related genetically (the Nei index would be close to 1 if the varieties brought many different alleles equally distributed among the varieties) as if the market, agricultural and regulatory contexts did not provide enough incentives to diversify.

ii) An increase in spatial homogenization. The number of cultivated varieties dramatically increased during this period (Fig. 1). However, while the cumulated frequency of the first five varieties at the national scale decreased (Fig. 2), the most frequent varieties became more related as illustrated by the Nei index of the five and ten major cultivars (Table S4) leading to an overall decline in H_T*. In addition, a lower among 'départements' variation was observed during this period for H_T*. This suggests that a limited number of genetically related cultivars were grown throughout France.

These developments can be related to an increased simplification and standardization of agricultural practices as well as to a narrowing of farmers' access to cultivars. As agricultural cooperatives merged with one another for economies of scale (this period is marked by such concentration, see Filippi et al., 2011), farmers from many different regions could have been affiliated with a same coop which provided only a limited number of cultivars.

4.2. Major regional differences identified and related to their agricultural history

Agricultural modernization, involving the replacement of landraces and 'old lines' by commercial cultivars and the genetic simplification of landscapes, did not happen simultaneously across the French countryside. Using a multivariate method of analysis of the H_T* values, 'départements' showing similar trends were clustered. The map showed that already by 1912, the regions where agriculture underwent an earlier 'modernization' (as elaborated earlier) such as the North-West quadrant, the Paris basin, and the west (groups 1, 2 and 3), had lower diversity than the other 'départements'. For these groups, H_T* values were respectively 0.52, 0.47 and 0.61 while they were 0.73, 0.91, 1.06 and 1.18 for groups 4, 5, 6 and 7 respectively. The latter regions (West Brittany, North-East and South-East quadrant, as well as in part of the South-West) cultivated more landraces in 1912 (respectively 77%, 81%, 86% and 97% compared to 30%, 70% and 56% for groups 1, 2 and 3 respectively). Overall, considering the seven groups in 1912, H_T* values were correlated to landrace frequencies ($R^2 = 0.63$) but the 'départements' where the landraces called 'Rouge de Bordeaux' and 'Noé' were dominant showed lower H_T* values (group 2 for example). This may be due to two mechanisms. First, these two landraces spread in the regions of most intensive farming and hence in 'départements' where a few cultivars already dominated. Second, most cultivated commercial 'old lines' were obtained from crosses involving 'Noé' as one parent (from which 'Rouge de Bordeaux' also originated *via* mass selection), hence leading to a lower among-varieties genetic diversity in 'départements' where these two landraces and common commercial cultivars co-located.

In the East and the South of France and in West Brittany (Groups 4, 5, 6, 7), agricultural 'modernization' occurred later (mostly after WWII) and it was not until the early 1960s that they experienced a complete replacement of landraces and "old lines" by "modern pure lines".

5. Conclusions

This study confirms the added value of the H_T* integrative indicator to monitor large scale, fine grain and long term trends in crop genetic diversity. From a methodological point of view, our results suggest that the number of varieties should not be used alone as an indicator to assess the evolution of crop genetic diversity. Such one-dimensional indicator should always be compared with and corrected by more integrative indexes such as H_T*. From an agronomic and environmental point of view, our report of a decrease of at least 50% of *in situ* wheat genetic diversity in the last century raises the issue of higher vulnerability and lower resilience in the face of faster and larger climatic changes including more stochastic year to year variation (Brisson et al., 2010). Biotic homogenization may have strong ecological and evolutionary effects on ecosystems functioning by reducing resilience to environmental changes (Díaz and Cabido, 2001; Olden et al., 2004). Moreover, crop diversity in agricultural fields (mixing genotypically diverse cultivars for example) is becoming recognized as a provider of a more stable food production (Kiaer et al., 2009) along with ecosystem services: for example; disease or pest regulation in Cheatham et al. (2009), Huang et al. (2012), Tooker and Frank (2012); biodiversity benefits in Whitham et al. (2006), Ninkovic et al. (2011), Chateil et al. (2013). It is thus likely that in-field crop genetic diversity will be a good factor for agricultural researchers to use in agroecological innovation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2014.06.003.

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