Genomic Enables Prediction in Maize Using Kernel Models with Genotype × Environment Interaction

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ABSTRACT Multi-environment trials are routinely conducted in plant breeding to select candidates for the next selection cycle. In this study, we compare the prediction accuracy of four developed genomic-enabled prediction models: (1) single-environment, main genotypic effect model (SM); (2) multi-environment, main genotypic effects model (MM); (3) multi-environment, single variance G×E deviation model (MDs); and (4) multi-environment, environment-specific variance G×E deviation model (MDe). Each of these four models were fitted using two kernel methods: a linear kernel Genomic Best Linear Unbiased Predictor, GBLUP (GB), and a nonlinear kernel Gaussian kernel (GK). The eight model-method combinations were applied to two extensive Brazilian maize data sets (HEL and USP data sets), having different numbers of maize hybrids evaluated in different environments for grain yield (GY), plant height (PH), and ear height (EH). Results show that the MDe and the MDs models fitted with the Gaussian kernel (MDe-GK, and MDs-GK) had the highest prediction accuracy. For GY in the HEL data set, the increase in prediction accuracy of SM-GK over SM-GB ranged from 9 to 32%. For the MM, MDs, and MDe models, the increase in prediction accuracy of GK over GB ranged from 9 to 49%. For GY in the USP data set, the increase in prediction accuracy of SM-GK over SM-GB ranged from 0 to 7%. For the MM, MDs, and MDe models, the increase in prediction accuracy of GK over GB ranged from 34 to 70%. For traits PH and EH, gains in prediction accuracy of models with GK compared to models with GB were smaller than those achieved in GY. Also, these gains in prediction accuracy decreased when a more difficult prediction problem was studied.

KEYWORDS Genotype × Environment interaction (G×E) Genomic Best Linear Unbiased Predictor (GBLUP) linear kernel Gaussian nonlinear kernel Genomic Selection GenPred Shared Data Resources

Genomic selection (GS) arose from the need to improve the prediction of complex traits based on dense marker information. It was first proposed in animal breeding (Meuwissen et al. 2001), and then applied to plant breeding (de los Campos et al. 2009; Crossa et al. 2010, 2011). Using GS, genomic breeding values are estimated as the sum of marker effects for unphentyped individuals in the testing population. Several genomic prediction models were developed and applied to simulated and real plant breeding data (Bernardo and Yu 2007; Massman et al. 2013; de los Campos et al. 2009, 2013; Crossa et al. 2010, 2011; Pérez-Rodríguez et al. 2013; Beyene et al. 2015). In general, these studies showed good prediction accuracies for complex traits evaluated by means of random cross-validation (CV) partitions of the data.

Genomic-enabled prediction models were originally developed for a single trait in a single environment. However, multi-environment plant breeding trials are routinely conducted to estimate and take advantage of genotype × environment interaction (G×E). Therefore, to implement GS strategies in plant breeding, G×E needs to be estimated, modeled, and predicted. When genetic marker information is used for computing
associations between individuals through the Genomic Relationships Matrix (GRM) G (Habier et al., 2007), this model is also referred to as Genomic Best Linear Unbiased Predictor (GBLUP) (VanRaden, 2007, 2008). Burgueño et al. (2012) extended the GBLUP methodology to incorporate and model G×E effects. The Bayesian model of Jarquin et al. (2014) is another GBLUP extension that introduces main and interaction effects of markers and environmental covariates via covariance structures. Heslot et al. (2014) proposed using crop modeling for assessing genomic G×E. In general, studies have shown that modeling G×E can give substantial gains in prediction accuracy (Burgueño et al. 2012; Heslot et al. 2014; Jarquin et al. 2014; Crossa et al. 2016a,b; Cuevas et al. 2016a).

Recently, López-Cruz et al. (2015) proposed a GBLUP prediction model that explicitly models G×E and marker × environment interaction (M×E) where marker effects and genomic values are partitioned into components that are stable across environments (main effects) and others that are environment-specific (interactions). The model of López-Cruz et al. (2015) has advantages and disadvantages; the advantages are: (i) it can be easily implemented using existing software for GS, for example, BGLR (de los Campos and Pérez-Rodríguez 2016); and (ii) it can be implemented using both shrinkage methods (a ridge-regression type estimator) and variable (marker) selection methods. In this case, the M×E model can be employed not only for GS but also for genome-wide association analyses to identify genomic regions that contribute to stability and to interaction effects (Crossa et al. 2016b). Furthermore, in terms of reducing the models’ residual variance, the M×E model outperformed the more traditional single-environment and across-environment models for complex traits (López-Cruz et al. 2015; Crossa et al. 2016b). However, the M×E model is more efficient when applied to sets of environments that have positive correlations. This limitation arises because the genetic covariance between any pair of environments is represented by the variance of the main effect, which forces the covariance between pairs of environments to be positive (López-Cruz et al. 2015).

VanRaden (2008) first suggested models using a standard linear kernel, where the GBLUP is a linear model characterized by parameters related to additive quantitative genetics theory. However, complex traits are affected by nonlinearity effects between genotypes and phenotypes due to complex interactions among genes (i.e., epistasis) and their interaction with the environment. Gianola et al. (2006) proposed nonparametric and semiparametric methods to model the relationship between the phenotype and markers that are available within the GS framework. The nonparametric methods are capable of accounting for small complex epistatic interactions without explicitly modeling them.

Therefore, the semi-parametric Reproducing Kernel Hilbert Space (RKHS) reduces the dimensions of the parametric space and also captures small complex interactions among markers (Gianola and van Kaam 2008; de los Campos et al. 2010; Morota and Gianola 2014; Gianola et al. 2006, 2014). The RKHS method uses a kernel function to convert the marker matrix into a set of distances between pairs of individuals (Heslot et al. 2012). Recently, Jiang and Reif (2015) formulated a model with explicit epistatic effects of markers and proved that this model is equivalent to RKHS with Gaussian kernel, thus demonstrating that this model captures epistatic effects among markers. Several studies confirmed the advantage of using RKHS regression to increase prediction accuracy by capturing nonadditive variation (de los Campos et al. 2010; Heslot et al. 2012; Morota et al. 2013; Pérez-Rodriguez et al. 2013; Morota and Gianola 2014). Recently, Cuevas et al. (2016a) compared methods that applied the G×E interaction GS model of López-Cruz et al. (2015) using a linear kernel (GBLUP) and a nonlinear Gaussian kernel with the bandwidth estimated by an empirical Bayes method proposed by Pérez-Elizalde et al. (2015), and a Kernel Averaging method, or multi Gaussian kernels. Morota and Gianola (2014) extended the GBLUP methodology to model the nonadditive variation (de los Campos et al. 2012; Morota 1996) using crop modeling to show the higher prediction ability of the Gaussian kernel models compared with the G×E model and the GBLUP model. The most flexible Gaussian kernels captured major and complex effects of markers in addition to their interaction effects.

In genomic-enabled prediction, linear models consider genetic values as linear combinations of marker effects; therefore, GBLUP with G×E can also be fitted with the nonlinear Gaussian kernel. Similarly, the model of Jarquin et al. (2014) can also be used with the linear GBLUP kernel, and with the nonlinear Gaussian kernel (GK). However, so far, the model of Jarquin et al. (2014) has not been used with the GK, and its prediction accuracy has not been compared with the G×E with the GBLUP kernel of López-Cruz et al. (2015), or with the model of Jarquin et al. (2014) across environments, or when including G×E with the GBLUP kernel.

Therefore, the main objectives of this research were: (1) to study the prediction accuracy of the multi-environment, single variance G×E deviation model (MDs) of Jarquin et al. (2014) used with the GK method (MDs-GK) and the prediction accuracy of the multi-environment, environment-specific variance G×E deviation model (MDe) of López-Cruz et al. (2015) fitted with the GK method (MDe-GK), and to compare them with the prediction accuracy of their counterpart models using the linear kernel GBLUP (GB) method (MDs-GB and MDe-GB), and (2) to compare the accuracy of the four previous models with the accuracy of the single-environment, main genotypic effect model (SM), and the multi-environment, main genotypic effect (MM) of Jarquin et al. (2014) using GB and GK methods (SM-GK, SM-GM, MM-GB, and MM-GB). Two data sets of Brazilian maize hybrids (HEL and USP) genotyped with dense molecular markers, and phenotyped in different environments with different numbers of hybrids per environment and different traits, were used to compare the prediction accuracy of those eight model-methods.

### MATERIALS AND METHODS

**Phenotypic experimental data**

This study considered two hybrid maize data sets. The first data set is from the Helix Seeds Company (HEL), while the second is from the University of São Paulo (USP). The HEL data set consists of 452 maize hybrids obtained by crossing 111 pure lines (inbreds); the hybrids were evaluated in 2015 at five Brazilian sites: Nova Mutum (NM), (13° 05’ S, 56° 05’ W, 460 m above sea level) and Sorriso (SO) (12° 32’ S, 55° 42’ W, 365 m above sea level) in the state of Mato Grosso; Pato de Minas (PM) (18° 34’ S, 46° 31’ W, 832 m above sea level), and Ipiacu (IP) (18° 41’ S, 49° 56’ W, 452 m above sea level) in the state of Minas Gerais; and Sertanópolis (SE) (23° 03’ S, 51° 02’ W, 361 m above sea level) in the state of Paraná. The experimental design was a randomized block with two replicates per genotype and environment. The phenotypic and genomic data on inbred lines are credited to Helix Seeds Ltda Company.

Data from USP consist of 740 maize hybrids obtained by crossing 49 inbred lines. The hybrids were evaluated at Piracicaba and Anhumas, São Paulo, Brazil, in 2016. The hybrids were evaluated using an augmented block design, with two commercial hybrids as checks to correct
for micro-environmental variation. At each site, two levels of nitrogen (N) fertilization were used: Ideal N (IN) and Low N (LN) for a total of four artificial environments (P-IN, P-LN, A-IN, and A-IN). The experiment conducted under ideal N conditions received 100 kg ha$^{-1}$ of N (30 kg ha$^{-1}$ at sowing and 70 kg ha$^{-1}$ in a coverage application) at the V8 plant stage, while the experiment with low N received 30 kg/ha of N at sowing. Each plot was 7 m in length, with 0.50 m spacing between rows and 0.33 m between plants.

There was an imbalance in both data sets because not all hybrids were evaluated in all locations (incomplete field trials). The main traits of the two data sets were GY (grain yield in ton per hectare), PH (plant height in centimeters), and EH (ear height in centimeters). Plant height was measured from the ground to the flag leaf and EH from the ground to the base of the ear. The empirical distribution of the three evaluated traits (GY, PH, and EH) were symmetric in most of the environments (Figure 1). For the HEL data set, PH and EH were evaluated in three environments. Broad sense heritability (repeatability) was computed using the standard formula based on plot means:

$$
\frac{\sigma_h^2}{\left[ \sigma_h^2 + \sigma_{s0}^2/s + \sigma_r^2/s r \right]},
$$

where $\sigma_h^2$ is the variance of the hybrids, $\sigma_{s0}^2$ is the variance of the hybrids $\times$ location interaction and $\sigma_r^2$ is the residual error variance and $s$ and $r$ are the number of environments and replications in each environment, respectively.

### Genotypic data

The USP and HEL parent lines were genotyped with an Affymetrix Axiom Maize Genotyping Array of 616 K SNPs (Unterseer et al. 2014). Standard quality controls (QC) were applied to the data, removing markers with a Call Rate $\leq 95$. The remaining missing data in lines were imputed with the Symbread package (Wimmer et al. 2015) using the algorithms from the software Beagle 4.0 (Browning and Browning 2008). The hybrid genotypes were obtained by genomic information of the parent inbred lines. Markers with Minor Allele Frequency (MAF) of $\leq 0.05$ were removed. After applying QC, 52,811 and 54,113 SNPs were available to make the predictions in the HEL and USP data sets, respectively.

### STATISTICAL MODELS

Statistical models for genomic predictions taking into account G×E were proposed by Jarquin et al. (2014) and López-Cruz et al. (2015). The Jarquin model incorporates genetic information from molecular markers or from pedigree (Pérez-Rodríguez et al. 2015), and/or from environmental covariates, whereas the López-Cruz model decomposes the marker effect across all environments and for each specific environment (interaction).

In this study, four statistical prediction models were fitted to both data sets to study their prediction accuracy using random CV schemes (Table 1). We also compared the prediction accuracy of two kernel regression methods in the four models. The models were: a single-environment, main genotypic effect model (SM), a multi-environment, main genotypic effect model (MM) (Jarquin et al. 2014), a multi-environment, single variance G×E deviation model (MDs) (Jarquin et al. 2014) and a multiple-environment environment-specific variance G×E deviation model (MDe) (López-Cruz et al. 2015). The two kernel regression methods were: the linear kernel GBLUP (GB) method used by Jarquin et al. (2014) and López-Cruz et al. (2015), and the Gaussian kernel (GK) method proposed by Cuevas et al. (2016a).

The single-environment, main genotypic effect model (SM)

The SM model fits the data from each environment separately and takes into account the main effect of genotypes. In matrix notation the model is written as:

$$
y = \mu_1 + Z_u u + \varepsilon
$$

where $y = (y_1, \ldots, y_n)'$ is the response vector, and $y_i$ represents the observations in the $i$th line ($i = 1, \ldots, n$) in each environment; $\mu$ is the general mean; $Z_u$ is the incidence matrix that connects the random genetic effects with phenotypes; $u$ is the random genetic effects for each environment, and $\varepsilon$ the residual random effects for each environment. The SM model (1) assumes that the distribution of the $u$ vector is multivariate normal with mean zero and a covariance matrix $\sigma_u^2 K$, that is, $u \sim N(0, \sigma_u^2 K)$. Where $\sigma_u^2$ is the genetic variance component of $u$ in the $j$th environment and $K$ is a symmetric, positive semi-definite matrix, denoting the variance–covariance of the genetic values constructed from the genomic molecular markers. It is also assumed that the errors $\varepsilon$ in each environment are independent with homogeneous variance, $\sigma_r^2$, and distributed as $\varepsilon \sim N(0, \sigma_r^2 I)$ (where $I$ is the identity matrix, and $\sigma_r^2$ is the residual variance in the
Table 1 Model, kernel method, and abbreviation of the model-method combination

| Modela                                                   | Kernel Method | Abbreviation |
|----------------------------------------------------------|---------------|--------------|
| Single-environment, main genotypic effect model (SM)     | GBLUP (GB)    | SM-GB        |
| \(y = \mu_1 + Z_u u + \varepsilon\)                     | Gaussian      | SM-GK        |
| Multi-environment, main genotypic effect (MM)            | GBLUP (GB)    | MM-GB        |
| \(y = \mu_1 + Z_i \beta_i + Z_u u + \varepsilon\)       | Gaussian      | MM-GK        |
| Multi-environment, single variance GxE deviation model (MDs) | GBLUP (GB)    | MDs-GB       |
| \(y = \mu_1 + Z_u u + \varepsilon\)                     | Gaussian      | MDs-GK       |
| Multi-environment, environment-specific variance GxE deviation model (MDe) | GBLUP (GB)    | MDe-GB       |
| \(y = \mu_1 + Z_i \beta_i + Z_u u_i + u_E + \varepsilon\) | Gaussian      | MDe-GK       |

aModel-methods are described in the section Materials and Methods.

The single-environment, main genotypic effect model with GBLUP (SM-GB) and Gaussian kernel (SM-GK)

For SM model (1), matrix \(K\) can be constructed using the linear kernel \(K = XX' / p\) (de los Campos et al. 2013) proposed by VanRaden (2007, 2008) for estimating the GBLUP, where \(X\) is the standardized matrix of molecular markers for the individuals, of order \(n \times p\), where \(p\) is the number of markers (Table 1).

When markers have a more complex function, the GK has proved to be more effective for capturing complex cryptic interactions between markers, thereby improving the prediction accuracy of the model (Cuevas et al. 2016a). The entries of the Gaussian kernel are computed as \(K(x_i, x_j) = \exp(-h d_{ij}^2)\), where \(d_{ij}\) is the Euclidean distance between the individuals \(i\)th and \(j\)th \((i = 1, \ldots, n_i)\) given by the markers; \(h > 0\) is the bandwidth parameter that controls the rate of decay of \(K\) values (Pérez-Rodríguez et al., 2012; Cuevas et al. 2016a). In this study, GK takes the form \(K(x_i, x_j) = \exp(-h d_{ij}/\text{median}(d_{ij}^2))\), where \(h = 1\) and the median of the distances is used as a scaling factor (Crossa et al. 2010). de los Campos et al. (2010) described the theory of the Gaussian kernel in the context of the kernel averaging method for the RKHS.

The multi-environment, main genotypic effect model (MM)

One multi-environment model considers the main fixed effects of environments, as well as the random genetic effects across environments

\[y = \mu_1 + Z_E \beta_E + Z_u u + \varepsilon\]  

where \(y = (y_1, \ldots, y_9)\) is the response vector and \(y_j\) is the vector of observations of the lines \((i = 1, \ldots, n_j)\) in the \(j\)th environment \((j = 1, \ldots, s)\). The fixed effects of the environment for the data used in this study are modeled with the incidence matrix of the environments \(Z_E\), where the parameters to be estimated are the intercept for each environment \((\beta_E)\) (other fixed effects can be incorporated into the model), and incidence matrix \(Z_u\) connects genotypes with phenotypes for each environment. It is assumed that the random vector of genetic effects \(u\) across environments follows a multivariate normal with mean zero and a covariance matrix \(\sigma_u^2 K\), that is, \(u \sim N(0, \sigma_u^2 K)\), where \(\sigma_u^2\) is the variance of the main genetic effects across environments, and \(\varepsilon \sim N(0, \sigma^2 I)\). In this case, the resulting model is equivalent to the across-environment GBLUP model of López-Cruz et al. (2015) and Jarquin et al. (2014). When in the MM model of (2) \(u\) is used with \(K = XX' / p\) (GBLUP), the model is the GBLUP across environments (MM-GB), whereas if \(u\) is used with the GK, the model is the GK across environments (MM-GK) (Table 1).

Multi-environment, single variance G\(\times\)E deviation model (MDs)

This model extends (2) by adding the random interaction effect of the environments with the genetic information of the lines \((u_E)\)

\[y = \mu_1 + Z_E \beta_E + Z_u u + u_E + \varepsilon\]  

It is assumed that the vector of random effects of the interaction \(u_E\) has a multivariate normal distribution, \(u_E \sim N(0, \sigma_{ue}^2 K)\), where \((\cdot)^{\circ}\) is the Haddamard product operator and denotes the element-to-element product between two matrices in the same order (Jarquin et al., 2014). \(\sigma_{ue}^2\) is the variance component of the interaction, the \(K\) matrix is defined as before, and \(u\) is the vector of the main genetic effects that follows a multivariate normal with mean zero and a covariance matrix \(\sigma_u^2 K\), that is, \(u \sim N(0, \sigma_u^2 K)\), where \(\sigma_u^2\) is the variance of the main genetic effects and \(\varepsilon \sim N(0, \sigma^2 I)\). Therefore, under these conditions

\[Z_u K Z_u^{\circ} = \begin{bmatrix} K_i & \cdots & 0 & \cdots & 0 \\
\vdots & \ddots & \vdots & \ddots & \vdots \\
0 & \cdots & K_j & \cdots & 0 \\
\vdots & \ddots & \vdots & \ddots & \vdots \\
0 & \cdots & 0 & \cdots & K_m \end{bmatrix}\]

where \(K_i\) represents the kernel constructed from the molecular markers of the lines in the \(i\)th environment. Just as in model (2), matrix \(K\) is used in the variance-covariance of \(u\) of model (3), and is also a component of the variance-covariance of \(u_E\). Then, kernel matrix \(K\) can be constructed using the linear kernel (MDs-GB) or the GK (MDs-GK) (Table 1).

Multi-environment, environment-specific variance G\(\times\)E deviation model (MDe)

The model of López-Cruz et al. (2015) separates the genetic effects of markers into the main marker effects across all environments and the specific marker effects in each environment. Thus, this model in matrix notation is

\[y = \mu_1 + Z_E \beta_E + Z_u u_0 + u_E + \varepsilon\]  

For the MDe model (4) of the vector, \(u_0\) represents the main effect of markers (across all environments) with a variance-covariance structure similar to those used in models (2) and (3), that is, \(u_0 \sim N(0, \sigma_0^2 K)\). However, as pointed out by López-Cruz et al. (2015) and Cuevas et al. (2016a), \(\sigma_0^2\) is common to all \(s\) environments, and the borrowing of information among environments is generated through kernel matrix \(K\). On the other hand, \(u_E\) represents the specific effect of the markers in environments (or the effects of the
interaction) with a variance–covariance structure different from model (3), that is, $u_{fi} \sim N(0, K_E)$, where $K_E$ is:

$$
K_E = \begin{bmatrix}
\sigma^2_{u1} K_1 & \cdots & 0 & \cdots & 0 \\
\vdots & \ddots & \vdots & \cdots & \vdots \\
0 & \cdots & \sigma^2_{u2} K_j & \cdots & 0 \\
\vdots & \ddots & \vdots & \cdots & \vdots \\
0 & \cdots & 0 & \cdots & \sigma^2_{um} K_m \\
\end{bmatrix}
$$

Note that matrix $K_E$ can be expressed as the sum of $s$ matrices, and the effects given by $u_{fi}$ are specific to the $f$th environment; thus, it has a normal distribution with mean and variance equal to 0, except for the $j$th environment, which has a variance–covariance matrix $\sigma^2_{uji} K_j$. The importance of these two terms ($u$ and $u_{fi}$) of MDe model (4) is given by the corresponding variance components that are estimated from the data. Kernel matrix $K$ is used in the components of $u$, while kernel matrix $K_E$ is used in the component of $u_{fi}$; both, $K$ and $K_E$ can be used with linear kernel (MDe-GB) or with the Gaussian kernel (MDe-GK) (Table 1).

### Estimating variance components using full data analyses

The four models—SM, MM, MDs, and MDe fitted with GBLUP and GK methods—were used on the entire HEL and USP data sets for all traits. To fit the models, the phenotypic data were centered and standardized (i.e., each phenotypic data point was centered by subtracting the overall mean of all environments and standardized by dividing by the sample standard deviation across all environments). These analyses were performed to derive estimates of variance components. The posterior variance components resulting from the residual effects, genetic main effect, and genetic environment-specific effects of the four models described above for three traits and for environments in HEL and USP data sets were computed and reported. Since the data were standardized for GBLUP method, the summation of the variance components approximates 1.

#### Assessing prediction accuracy by random CV

The prediction accuracy of the single-environment model-methods was assessed using 50 random partitions, organized in five folds with 10 random partitions each, with 80% of the hybrids comprising the training (TRN) set, and the remaining 20% of the individuals comprising the testing (TST) set. This was performed separately in each environment, as the single-environment models were fitted separately for each environment. For this validation procedure, all the parameters of the models (including variance components resulting from residual effects, and genetic effects) were re-estimated from TRN data in each of the TRN-TST partitions.

For the multi-environment models, the prediction accuracy of the model-methods for predicting the pattern of missing values in each environment was generated using two different CV designs (Burgueño et al. 2012). The random CV1 design mimics the prediction problem faced by breeders when newly developed lines have not been evaluated in any environment; in this case, 20% of the lines were not observed (unphenotyped) in all the environments and had to be predicted. The random CV2 design mimics a prediction problem when lines are tested in incomplete field trials (sparse testing), where some lines are evaluated in some environments but not included in other environments. For these approaches, we assigned 80% of the observations to TRN and 20% to TST. None of the lines to be predicted in the TST are in the TRN set. For this validation procedure, all the parameters of the models (including variance components resulting from residual effects, genetic main effects, genetic × environment interactions effects, and environment-specific effects) were re-estimated from TRN data in each of the 50 random TRN-TST partitions. Note that CV2 design can only be applied to single-environment model-methods (MM, MDs, and MDe), but not to multi-environment model-methods (SM). Also, for SM the random CV is a CV1 but applied to only one individual environment (site).

For each TRN-TST partition, models were fitted to the TRN data set, and prediction accuracy was assessed by computing Pearson’s correlation coefficient between the predicted values and the observed values in the TST set. The correlation coefficient was used as a measure of prediction accuracy, with values close to 1 indicating a high level of accuracy.

### Table 2 Heritability and phenotypic correlations among five environments for grain yield, and three environments for plant height and ear height for the HEL data set

| Site          | Ipiaçu | Nova Mutum | Pato de Minas | Sertanópolis | Sorriso | Grain yield | Heritability |
|---------------|--------|------------|---------------|--------------|---------|-------------|--------------|
| Nova Mutum    | 0.46   | —          | —             | —            | —       | —           | —            |
| Pato de Minas | 0.51   | 0.44       | —             | —            | —       | —           | —            |
| Sertanópolis  | 0.29   | 0.36       | 0.30          | —            | —       | —           | —            |
| Sorriso       | 0.43   | 0.48       | 0.39          | 0.38         | —       | —           | —            |

Lower diagonal, plant height; upper diagonal, ear height.

| Trait         | Site          | Correlation |
|---------------|---------------|-------------|
| Grain yield   | Ipiaçu        | 0.81        |
|               | Nova Mutum    | 0.60        |
|               | Pato de Minas | 0.86        |
|               | Sertanópolis  | 0.69        |
|               | Sorriso       | 0.78        |
| Plant height  | Ipiaçu        | 0.72        |
|               | Nova Mutum    | —           |
|               | Pato de Minas | 0.86        |
|               | Sertanópolis  | 0.91        |
|               | Sorriso       | —           |
| Ear height    | Ipiaçu        | 0.69        |
|               | Nova Mutum    | —           |
|               | Pato de Minas | 0.81        |
|               | Sertanópolis  | 0.89        |
|               | Sorriso       | —           |
product–moment correlation between predictions and phenotypes in the TST data set within environments. The same TRN–TST partitions were used to assess the prediction accuracy of each of the models. Thus, 50 correlations were computed for each model and trait; the mean and SDs of these 50 correlations are reported.

Therefore, adjusting models for full data, making inference on the parameters, and assessing predictions in TRN–TST partitions were based on 30,000 samples collected from the posterior and predictive distributions after discarding 5000 samples as burn-in.

Software
The aforementioned models can be implemented using the R (R Core Team 2016) package Bayesian generalized linear regression (BGLR) (de los Campos and Pérez-Rodríguez 2016; Pérez-Rodríguez and de los Campos 2014). Appendix A gives the R codes used in the models in- cluded in this study when the numbers of individuals in different environments vary. It should be pointed out that, in previous studies using the Jarquin et al. (2014) and López-Cruz et al. (2015) models, the number of entries in each environment was the same; thus, the model fitting and the random CV partition scheme were simpler than in this case, where there are different numbers of entries in different environments.

Data availability
The phenotypic and genotypic data for the maize hybrids included in this study can be found at http://hdl.handle.net/11529/10887. Each HEL and USP data set contains the data corresponding to each GB and GK kernel, as well as phenotypic data for each trait (PH, EH, and GY) in each environment.

RESULTS

Descriptive statistics
Box-plots of GY, PH, and EH in each environment for the two data sets are depicted in Figure 1. Most of the distributions of the traits in environments had a symmetric distribution. For the HEL data set, environments NM and PM produced better GY, while environment SE had the lowest GY (Figure 1A). Traits PH and EH showed similar trends, but were measured in only three environments: IP, PM, and SE. Data from USP had environments with soil nutritional stress, and the results showed that environments with ideal nitrogen conditions (P–IN and A–IN) had better potential for all traits (Figure 1A).

All pair–wise environments for all traits in the HEL and USP data sets had high and positive correlations (Table 2 and Table 3). As expected, for PH and EH, the correlations were higher than for the complex trait GY. In all environments, GY, PH, and EH showed high heritability in the HEL data set: GY ranged from 0.60 to 0.86, PH varied from 0.72 to 0.91, and EH ranged from 0.69 to 0.89. For the USP data set, heritability values were high for PH and EH in all environments (from 0.60 to 0.85 and 0.66 to 0.91, respectively). For the USP data set, trait GY had an intermediate value of 0.42 for sites Anhumas and Piracicaba with ideal nitrogen (IN) and lower values for Piracicaba and Anhumas under low nitrogen conditions (LN) (0.22 and 0.19, respectively).

Estimating variance components
The distribution of the residuals after fitting the eight model-method combinations to the two data sets was approximately normal (data not shown). Phenotypic (and marker) data were standardized; thus summation of variance components approximated 1 for GB models. Devia- tions may be due to the high degree of imbalance in the number of hybrids in different environments, especially for data set HEL.

HEL data set

Single-environment: For the SM model for the three traits in each environment, the estimated residual variance components for the GK method were smaller than those for the GB method (Table 4). In contrast, the variance component of genetic effects for each environment increased for the SM–GK model-method as compared to the genetic effects of model-method SM–GB.

Multi-environment: For the MM model, the residual variance components for MM–GK were smaller than the residuals for MM–GB for all traits, whereas, for the genetic effects, the opposite occurred: the variance component of MM–GK was higher than that of MM–GB. For the MDs models, the residual variance components for MDs–GK were always smaller than the residual variances for MDs–GB, whereas the opposite occurred for the genetic main effect and genetic interaction effect (Table 4).

The results of the MM and MDs models indicated that the inclusion of the interaction term (G×E) induced a larger reduction in the estimated residual variance for GY; for traits PH and EH, these reductions in residual variance were smaller than those found for GY from the MM and MDs models. For the MDe model, the residual variance components for MDe–GK were smaller than those of the MDe–GB for all traits, whereas the variance components for the genetic main effect and genetic environment specific effect were higher for the GK models than for the GB model. The genetic main effect values are related to the
| Component                      | Environment | Grain Yield | Plant Height | Ear Height |
|-------------------------------|-------------|-------------|--------------|------------|
|                               |             | SM-GB       | SM-GK        | SM-GB      | SM-GK      |
| Residual $(\sigma^2_i)$       |             |             |              |            |
| Ipiaçú                        |             | 0.476 (0.05)| 0.259 (0.05)| 0.397 (0.05)| 0.243 (0.05)| 0.419 (0.05)| 0.246 (0.05) |
| Nova Mutum                    |             | 0.715 (0.06)| 0.431 (0.07)| —          | —          | —          | —          |
| Pato de Minas                 |             | 0.440 (0.03)| 0.221 (0.03)| 0.332 (0.03)| 0.151 (0.02)| 0.330 (0.03)| 0.163 (0.02) |
| Sertanópolis                 |             | 0.761 (0.07)| 0.467 (0.07)| 0.341 (0.05)| 0.198 (0.03)| 0.387 (0.03)| 0.225 (0.03) |
| Sorriso                       |             | 0.742 (0.07)| 0.467 (0.07)| —          | —          | —          | —          |
| Genetic effect $(\sigma^2_u)$ |             |             |              |            |
| Ipiaçú                        |             | 0.442 (0.10)| 0.965 (0.13)| 0.794 (0.17)| 1.231 (0.23)| 0.726 (0.18)| 1.221 (0.20) |
| Nova Mutum                    |             | 0.391 (0.12)| 1.177 (0.27)| —          | —          | —          | —          |
| Pato de Minas                 |             | 0.462 (0.09)| 1.106 (0.15)| 0.884 (0.16)| 1.331 (0.15)| 0.903 (0.16)| 1.278 (0.15) |
| Sertanópolis                 |             | 0.290 (0.09)| 1.156 (0.27)| 0.855 (0.14)| 1.224 (0.17)| 0.736 (0.16)| 1.199 (0.17) |
| Sorriso                       |             | 0.299 (0.09)| 1.132 (0.25)| —          | —          | —          | —          |
| Multi-environment, main genotypic effect (SM) | | | | |
| Residual $(\sigma^2_e)$       |             | 0.336 (0.01)| 0.273 (0.01)| 0.324 (0.02)| 0.259 (0.01)| 0.299 (0.013)| 0.222 (0.01) |
| Genetic main effect $(\sigma^2_u)$ | | 0.129 (0.03)| 0.316 (0.041)| 0.758 (0.12)| 0.769 (0.08)| 0.802 (0.13)| 0.846 (0.08) |
| Genetic Interaction effect $(\sigma^2_{ue})$ | | 0.111 (0.014)| 0.244 (0.24)| 0.04 (0.01)| 0.124 (0.03)| 0.051 (0.01)| 0.155 (0.01) |
| Multi-environment, main genotypic effects (MM) | | | | |
| Residual $(\sigma^2_e)$       |             | 0.230 (0.00)| 0.107 (0.01)| 0.274 (0.013)| 0.164 (0.01)| 0.294 (0.014)| 0.188 (0.01) |
| Genetic main effect $(\sigma^2_u)$ | | 0.122 (0.030)| 0.375 (0.04)| 0.798 (0.13)| 0.844 (0.08)| 0.763 (0.13)| 0.764 (0.08) |
| Genetic environment specific effect $(\sigma^2_{ue})$ | | 0.111 (0.014)| 0.244 (0.24)| 0.04 (0.01)| 0.124 (0.03)| 0.051 (0.01)| 0.155 (0.01) |

Estimates of different variance components for single-environment, main genotypic effect GBLUP kernel (SM-GB), single-environment, main genotypic effect GK (SM-GK), multi-environment, main genotypic effect GBLUP kernel (MM-GB), multi-environment, main genotypic effect GK (MM-GK), multi-environment, single variance G\(\times\)E deviation model GBLUP kernel (MDs-GB), multi-environment, single variance G\(\times\)E deviation model GK (MDs-GK), multi-environment, environment-specific variance G\(\times\)E deviation model GBLUP kernel (MDe-GB), multi-environment, environment-specific variance G\(\times\)E deviation model GK (MDe-GK) for three traits: grain yield, plant height and ear height.
## Table 5 USP data set

| Component                                      | Environment | Grain Yield | Plant Height | Ear Height |
|------------------------------------------------|-------------|-------------|--------------|------------|
|                                                 |             | SM-GB       | SM-GK        | SM-GB      | SM-GK      | SM-GB      | SM-GK      |
| Residual ($\sigma_i^2$)                        | P-LN        | 0.878 (.04) | 0.797 (.05) | 0.749 (.04) | 0.656 (.04) | 0.503 (.03) | 0.377 (.03) |
|                                                | P-IN        | 0.851 (.05) | 0.786 (.05) | 0.685 (.04) | 0.594 (.04) | 0.492 (.03) | 0.376 (.03) |
|                                                | A-LN        | 0.873 (.05) | 0.817 (.05) | 0.812 (.04) | 0.726 (.05) | 0.627 (.03) | 0.513 (.04) |
|                                                | A-IN        | 0.780 (.04) | 0.699 (.05) | 0.654 (.03) | 0.543 (.04) | 0.494 (.03) | 0.375 (.03) |
| Genetic effect ($\sigma_u^2$)                   | P-LN        | 0.132 (.04) | 0.438 (.12) | 0.257 (.07) | 0.619 (.13) | 0.556 (.13) | 0.955 (.15) |
|                                                | P-IN        | 0.149 (.05) | 0.420 (.10) | 0.341 (.08) | 0.683 (.14) | 0.537 (.12) | 0.829 (.15) |
|                                                | A-LN        | 0.124 (.04) | 0.366 (.09) | 0.188 (.05) | 0.523 (.14) | 0.397 (.10) | 0.808 (.07) |
|                                                | A-IN        | 0.232 (.06) | 0.550 (.12) | 0.383 (.09) | 0.747 (.14) | 0.549 (.12) | 0.922 (.08) |
| Residual ($\sigma_i^2$)                        | MM-GB       | 0.864 (.02) | 0.656 (.02) | 0.705 (.02) | 0.319 (.01) | 0.519 (.01) | 0.279 (.01) |
| Genetic main effect ($\sigma_u^2$)             | MM-GB       | 0.167 (.04) | 1.39 (.16)  | 0.341 (.07) | 3.131 (.22) | 0.56 (.12)  | 1.861 (.14) |
| Genetic interaction effect ($\sigma_{ue}^2$)   | MM-GK       | 0.024 (.01) | 0.094 (.02) | 0.008 (.00) | 0.057 (.01) | 0.019 (.01) | 0.073 (.01) |

### Multi-environment, main genotypic effects (MM)

| Residual ($\sigma_i^2$)                        | MDs-GB      | 0.836 (.02) | 0.536 (.02) | 0.699 (.02) | 0.304 (.01) | 0.509 (.01) | 0.264 (.01) |
| Genetic main effect ($\sigma_u^2$)             | MDs-GB      | 0.170 (.04) | 1.965 (.18) | 0.343 (.08) | 3.09 (.21)  | 0.547 (.12) | 1.819 (.13) |
| Genetic interaction effect ($\sigma_{ue}^2$)   | MDs-GB      | 0.024 (.01) | 0.094 (.02) | 0.008 (.00) | 0.057 (.01) | 0.019 (.01) | 0.073 (.01) |

### Multi-environment, single variance GxE deviation (MDs)

| Residual ($\sigma_i^2$)                        | MDe-GB      | 0.840 (.02) | 0.536 (.02) | 0.705 (.02) | 0.305 (.01) | 0.517 (.01) | 0.261 (.01) |
| Genetic main effect ($\sigma_u^2$)             | MDe-GB      | 0.170 (.04) | 1.966 (.19) | 0.340 (.08) | 3.168 (.22) | 0.558 (.12) | 1.894 (.13) |
| Genetic interaction effect ($\sigma_{ue}^2$)   | MDe-GB      | 0.024 (.01) | 0.094 (.02) | 0.008 (.00) | 0.057 (.01) | 0.019 (.01) | 0.073 (.01) |

### Multi-environment, environment-specific variance GxE deviation (MDe)

| Residual ($\sigma_i^2$)                        | MDe-GB      | 0.840 (.02) | 0.536 (.02) | 0.705 (.02) | 0.305 (.01) | 0.517 (.01) | 0.261 (.01) |
| Genetic main effect ($\sigma_u^2$)             | MDe-GB      | 0.170 (.04) | 1.966 (.19) | 0.340 (.08) | 3.168 (.22) | 0.558 (.12) | 1.894 (.13) |
| Genetic interaction effect ($\sigma_{ue}^2$)   | MDe-GB      | 0.024 (.01) | 0.094 (.02) | 0.008 (.00) | 0.057 (.01) | 0.019 (.01) | 0.073 (.01) |

Estimates of different variance components for single-environment, main genotypic effect GBLUP kernel (SM-GB), single-environment, main genotypic effect GK (SM-GK), multi-environment, main genotypic effect GBLUP kernel (MM-GB), multi-environment, main genotypic effect GK (MM-GK), multi-environment, single variance GxE deviation model GK (MDs-GK), multi-environment, environment-specific variance GxE deviation model GBLUP kernel (MDe-GB), multi-environment, environment-specific variance GxE deviation model GK (MDe-GK) for three traits: grain yield, plant height and ear height.

Environments: A-IN, Anhumas ideal N; A-LN, Anhumas low N; P-IN, Piracicaba ideal N; P-LN Piracicaba low N.
correlations between environments, which are positive and range from medium to high. For the variance component associated with the genetic interaction effect, the values are lower because they decreased GxE in environments with a positive correlation. In general, the fit of MDs is slightly worse than the fit of MDe models because the genetic interaction effect component has a small effect on all traits, but mainly on EH and PH (Table 4).

**USP data set**

**Single-environment:** For all traits, the variance components of genetic effects were higher when using the GK than the GB method in all environments and traits for the single-environment, main genotypic effect model (SM) (Table 5). The residual variance for SM-GK was always smaller than the residual for SM-GB for all traits.

**Multi-environment:** The residual variance components of the MM and MDs models for all traits were very similar, as were most of the variance components for the genetic main effects. For all the environments and traits, the residuals from the GK were smaller than the residuals from the GB for the MM, MDs, and MDe models. The variance components of the genetic main effects of MDs-GB and MDe-GB were consistently smaller than the genetic main effect of model-methods MDs-GK and MDe-GK. Also, the variance components of the genetic environment specific effects of the GK models were higher than those of the GB models for all traits (Table 5).

**Prediction accuracy of the models with GBLUP and GK methods**

Results of the prediction accuracy of the eight model-method combinations for the random CV2 of the two data sets are given in Figure 2, Figure 3, Figure 4, Figure 5, Table 6, and Table 7. Results of the prediction accuracy of the eight model-method combinations for random CV1 of the two data sets are given in Table B1 and Table B2 in Appendix B. Note that, for the single-environment models, prediction accuracy was assessed by 50 random partitions of the data into 80% TRN and 20% TST.

**HEL data set**

**Single-environment:** Results for CV2 for GY showed that the prediction accuracy of the SM-GK model-method was higher than for SM-GB in all environments (Figure 2). For GY in environment IP, prediction accuracies were 0.64 for SM-GB and 0.73 for SM-GK, while in environment PM, prediction accuracies were 0.68 for SM-GB and 0.74 for SM-GK (Table 6). The percent change in accuracy for single-environment GB vs. single-environment GK for GY ranged from 9 to 32% for the PM and NM environments, respectively. For trait PH, prediction accuracies were high: >0.65 for SM-GB and >0.69 for SM-GK. For trait EH, prediction accuracies were >0.64 for SM-GB and >0.67 for SM-GK; the increase in prediction accuracy ranged from 3% to 6% for traits EH and PH (Table 6).

**Multi-environment:** For GY, the best model-methods for CV2 were MDs-GK and MDe-GK for the five environments, followed by MDs-GB in the IP environment, MM-GK in the NM, PM, and SO environments and by MDs-GB and MDe-GB in the SE environment (Figure 3). For trait GY, the percent change in accuracy for MM-GB vs. MM-GK was high, ranging from 9% in PM to 48% in SE environment; for MDs-GB vs. MDs-GK, the % change ranged from 13% in PM to 47% in the SO environment; and for MDe-GB vs. MDe-GK, the % change ranged from 13% in PM to 49% in SE environment (Table 6). These results show that, for trait GY, the increase in prediction accuracy was high using the GK method. For less complex traits PH and EH, the percent change of GK over GB for all models showed a small increase in prediction accuracy, with the percent change ranging from 1 to 6%; there was no difference for trait EH in the IP environment.

For GY, models MDs-GK and MDe-GK were, for CV2, the models that had the best prediction accuracy in all environments, with values ranging from 0.58 in SE to 0.81 in the IP environment. These values were higher for a complex trait like GY (Figure 3). For the PH trait, MDs-GK and MDe-GK were the best models, with a prediction accuracy of 0.81–0.82 for all environments; for trait EH, these values ranged from 0.77 in IP to 0.81 in PM. In general, MDs models had similar results across environments. Prediction accuracy for random CV1 decreased (Table B1, Appendix B) as compared with those computed for CV2 for all traits and models. For example, for environment IP, MM-GB in CV2 gave a correlation of 0.56, whereas for CV1, prediction accuracy was 0.48, that is, an 8% decrease in accuracy, whereas, for environment NM, the decrease is ~10%. Similar decreases in accuracy from CV1 to CV2 were found for other traits and model-method combinations. However, for GY,
models with GK showed a greater increase in prediction accuracy over models with GB under CV1 (Table B1, Appendix B) than the increases achieved by those models under CV2 (Table 6). The % change in prediction accuracy of CV1 vs. CV2 for models with method GK vs. GB did not change for traits PH and EH.

**Summary of results:** Prediction accuracy of trait GY in the five testing environments increased from 9 to 48% for models with method GK compared to models with method GB. For GY, increases in prediction accuracy of environments from multi-environment models MM, MDs, and MDe with GK vs. MM, MDs, and MDe with GB tended to be higher than those achieved by the single-environment model (SM-GK vs. SM-GB). For traits PH and EH in three environments, the increase in prediction accuracy of method GK over method GB ranged only from 0 to 6%, and increases in prediction accuracy from multi-environment models MM, MDs, and MDe with GK vs. MM, MDs, and MDe with GB tended to be lower than those achieved by the single-environment model (SM-GK vs. SM-GB).

Although prediction accuracy for all model-method combinations decreased in CV1 vs. CV2, the % change in the prediction accuracy of

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**Figure 3** HEL data set. Mean correlation between observed and predictive values (average of 50 random CV partitions, CV2) for multi-environment, main genotypic effect model GBLUP kernel (MM-GB), multi-environment, main genotypic effect GK (MM-GK), multi-environment, single variance GxE deviation model GBLUP kernel (MDs-GB), multi-environment, single variance GxE deviation model GK (MDs-GK), multi-environment, environment-specific variance GxE deviation model GBLUP kernel (MDe-GB), multi-environment, environment-specific variance GxE deviation model GK (MDe-GK) for (A) five environments (horizontal axis) for grain yield, (B) three environments for plant height, and (C) three environments for ear height. Environments are: Ipiacu (IP), Nova Mutum (NM), Pato de Minas (PM), Sertanopolis (SE) and Sorriso (SO). Error bars show SD.
models with GK vs. models GB did not change and even increased for GY.

**USP data set**

**Single-environment**: Table 7 shows the correlations between observed and predicted values for all models in the USP data set. In general, for traits GY, PH, and EH, all prediction accuracies of the single-environment models were similar using the GB or GK methods (Figure 4). In these cases, the percentage change in accuracy for SM-GB vs. SM-GK was 7% (GY) in environment P-LN and 5% (PH) in environment A-LN. For GY, the prediction accuracy in the A-IN environment (0.40 for SM-GB and SM-GK) was greater than in other environments. Gains in prediction accuracy of SM-GK over SM-GB for trait GY in this data set are much lower than those achieved in the HEL data set.

**Multi-environment**: Between the GB and GK methods, there were large increases in prediction accuracy using the GK method, especially for traits GY and PH (Figure 5). For trait GY, the MM model gave a high percentage change in accuracy for GB vs. GK ranging from 34 to 59%. In the MDs model, the percentage change ranged from 35 to 65%, and for the MDe model, the percentage change ranged from 37 to 70% (Table 7).

For PH, the increase using the GK method was similar to those found for the GY trait. The percentage change for the MM model with GB vs. GK ranged from 38% (A-IN and P-IN) to 57% (A-LN). For the MDs models, the percentage change ranged from 37% (A-IN) to 61% (A-LN), and, for the MDe models, the percentage change ranged from 37% (A-IN) to 51% (A-LN). For trait EH, the increase was smaller, ranging from 15 to 23% for the GBLUP vs. the GK method. The MM and MDs models showed similar correlations when compared using the same kernel method. Models MDs-GK and MDe-GK had a clear and sustainable increase in prediction accuracy over their counterparts using the GB kernel, MDs-GB, and MDe-GB.

The prediction accuracy of random CV1 decreased (Table B2, Appendix B) compared to the accuracy obtained with CV2 for all traits and models. In general, compared with other models, models MDs and MDe decreased the accuracy of CV1 vs. CV2 more; this was more pronounced for GY in some environments than in other environments. Also, the decrease in the accuracy of CV1 vs. CV2 was higher for GY than for PH and EH.

**Summary of results**: The prediction accuracy of trait GY in four environments increased from 34 to 70% for multi-environment models MM, MDs, and MDe with GK vs. MM, MDs, and MDe with GB. These gains in accuracy were much higher than those achieved by single-environment SM-GK over SM-GB (from 0 to 7%). Similar patterns were found for traits PH and EH, where the increase in prediction accuracy of method GK over method GB ranged from ~2 to 5% for the single-environment model, SM, and drastically increased for multi-environment models MM, MDs, and MDe with GK vs. MM, MDs, and MDe with GB, ranging from 15 to 57%.

Prediction accuracy for all model-method combinations decreased in CV1 vs. CV2 and the % change in accuracy of models with GK vs. models with GB decreased for all three traits. The increase in accuracy of models with GK vs. models with GB did not occur under the CV1 design.

**DISCUSSION**

Several studies have documented the benefits of using a nonlinear Gaussian kernel in multi-environment models for capturing small complex interactions among markers, and increasing prediction accuracy (Gianola et al. 2006, 2014; Crossa et al. 2010; Pérez-Rodríguez et al. 2013; Pérez-Elizalde et al. 2015; Cuevas et al. 2016a,b). In this research, genome-enabled prediction accuracy was studied in two different hybrid maize data sets using multi-environment models with the GBLUP and GK methods. In this context, we proposed including the GK in the model of Jarquin et al. (2014), which accounts for environment information without and with interaction terms. Prediction accuracy was obtained using traits with different genetic architecture and heritability values that ranged from low to high.

**Prediction accuracy differences in datasets, methods, CV designs and G×E**

We compared the single-environment model with two G×E models. The first G×E model can accommodate environmental covariables (Jarquin
et al. 2014) that were not available in this study; the second G×E model (López-Cruz et al. 2015) accommodates environment main effects and environment-specific variances; both models used the GB and GK methods proposed by Cuevas et al. (2016a). These two G×E models have demonstrated good prediction accuracy when used in genomic-enabled prediction studies (López-Cruz et al. 2015; Zhang et al. 2015; Crossa et al. 2016a; Saint Pierre et al. 2016). We found that GK methods improved the prediction ability of all single-environment and multi-environment models for CV2 design for all traits in HEL and USP datasets. Prediction of all traits with multi-environment models incorporating the G×E term, and the GK method gave better prediction accuracy (especially for complex traits such as GY) than the other model-methods. The increases in prediction accuracy using models with GK under random (CV2) are also reflected under random cross-validation 1 (CV1) for HEL data set, but, to a lesser extent due to the difficulty of borrowing information of unobserved (unpheno-typed) lines in all environments. Similar decreases in prediction accuracy were found by López-Cruz et al. (2015), when attempting to predict wheat lines in untested (unobserved) environments under the CV1 random partition scheme.

**Figure 5** USP data set. Mean correlation between observed and predictive values (average of 50 random CV partitions, CV2) for multi-environment, main genotypic effect model GBLUP kernel (MM-GB), multi-environment, main genotypic effect Gaussian kernel (MM-GK), multi-environment, single variance G×E deviation model GBLUP kernel (MDs-GB), multi-environment, single variance G×E deviation model Gaussian kernel (MDs-GK), multi-environment, environment-specific variance G×E deviation model GBLUP kernel (MDe-GB), multi-environment, environment-specific variance G×E deviation model Gaussian kernel (MDe-GK) in four environments (horizontal axis) for: (A) grain yield, (B) plant height, and (C) ear height. Environments: Anhumas ideal Nitrogen (A-IN), Anhumas low Nitrogen (A-LN), Piracicaba ideal Nitrogen (P-IN), and Piracicaba low Nitrogen (P-LN). Error bars show SD.
Furthermore, for trait GY, differences in CV1 vs. CV2 for GB and GK methods for the two data sets might also be due to other factors such as:

(1) Differences in dataset repeatability, higher in HEL data sets (0.81, 0.60, 0.86, 0.69, and 0.78 for each of the five environments) than in USP (0.22, 0.42, 0.19, and 0.42 for each of the four environments) (Table 2 and Table 3, respectively) due to better quality of the replicated trials in HEL than the unreplicated trials in USP;

(2) More opportunity to borrow information from the close relatives hybrids in HEL (genetic diversity = 0.175) than from the less related hybrids included in USP dataset (genetic diversity = 0.372). For $h = 1$ (bandwidth parameter) the GK is a direct function of the squared Euclidean distance between hybrids based on markers ($d_e$). Thus, for a set of unrelated hybrids $d_e \rightarrow$ large and $K \rightarrow I$ (identity matrix), i.e., the GK weight more heavily the within (own) hybrid information compared to the between hybrid (from relatives) information than GB (the marker information is of no use) (de los Campos et al. 2010). On the other hand, for a set of related hybrids then $d_e \rightarrow 0$ and $K \rightarrow I$ (matrix of ones), i.e., marker information given by the GK weight equally or less the own hybrid information compared to information from relatives given by GB. Therefore, we speculate that, for related hybrids of HEL dataset, GK gives heavier weights to the within hybrid as well as between hybrids than the GB method does, that is why for GY, CV1 and CV2 for the multi-environment models gave very good increase in prediction accuracy over the GB;

(3) For CV2, GxE modulates both values (within and between hybrid information); hybrids in USP (doubled the genetic diversity) less related than those from HEL data set, then it is expected negligible values between hybrids, and similar values assign by GK and GB to within hybrid information; for CV2, predictions accuracy depends, to a great extent, on the correlations between environments.

In summary, for CV2, for the prediction accuracy of GY in the HEL dataset, the method GK weights own, and between hybrid, performance as well as the relationship between environment (GxE modeled by MDs and MDe), whereas, for USP, GK weights only the own hybrid performance and the relationship between environment becomes more important that in the HEL data set.

In the studies of López-Cruz et al. (2015) and Cuevas et al. (2016a), the data were balanced in the sense that all the individuals were included at the same time in all the environments. On the contrary, in this study, we had a great deal of imbalance because different numbers of maize hybrids were included in different environments; this was more pronounced in the HEL data set than in the USP data set, and different R scripts were necessary for implementing the model–method combinations.
| Trait           | Method/Model | GB (% change) | MDe (% change) | MDs (% change) |
|-----------------|--------------|---------------|----------------|----------------|
| Grain yield     | GB-GB        | 0.27 (0.04)   | 0.29 (0.06)    | 0.32 (0.05)    |
|                 | GB-GK        | 0.34 (0.07)   | 0.43 (0.07)    | 0.43 (0.07)    |
|                 | GB-MM        | 0.34 (0.07)   | 0.55 (0.06)    | 0.51 (0.05)    |
|                 | GB-MDe-GB    | 0.34 (0.07)   | 0.55 (0.06)    | 0.51 (0.05)    |
|                 | GB-MDe-GK    | 0.34 (0.07)   | 0.55 (0.06)    | 0.51 (0.05)    |
|                 | GB-MMDs-GB   | 0.34 (0.07)   | 0.55 (0.06)    | 0.51 (0.05)    |
|                 | GB-MMDs-GK   | 0.34 (0.07)   | 0.55 (0.06)    | 0.51 (0.05)    |

The increase was not higher due to the occurrence of intermediate-to-high positive correlations between the analyzed environments, resulting in low GxE. These results corroborate those obtained by López-Cruz et al. (2015) and Cuevas et al. (2016a), who observed that the intensity of the environmental correlation is related to the proportion of the genomic variance explained by the genetic main effects of markers across environments and genetic-specific effects of markers in environments.

**Better fit of the GxE GK models**

For GY of the HEL data set, the better fit of the model-method MDe-GB over the MDs-GB and MM-GB models is evident in their residual variance components: 0.227, 0.230, and 0.336, respectively. Similarly, for GY of the USP data set, the better fit of model MDe-GK over the MDs-GK and MM-GK models is also evident in their residual variance components: 0.093, 0.107, and 0.273, respectively. These trends in the residuals of the models are also found in traits PH and EH. The residuals of GK models were lower than those of the GBLUP models, indicating the better fit of the nonlinear vs. the linear kernel methods.

For GY of the USP data set, similar trends in the residuals of model-method MDe-GB vs. the MDs-GB and MM-GB models were found: 0.840, 0.836, and 0.864, respectively. Similar clear trends in the residuals of these models were found for traits PH and EH. These patterns are also clear for the residuals of GK model-methods MDe-GK, MDs-GK, and MM-GK for trait EH, but not for trait PH.

**Prediction accuracy using multi-environment models**

In this study, all pairwise correlations between environments were high and positive. This is important, because the GxE model of López-Cruz et al. (2015) has the limitation of better and more efficient prediction when applied to subsets of environments that have positive and similar correlations (Crossa et al. 2016b; Cuevas et al. 2016a). In positively correlated environments, the main marker effects are the most influential components when predicting genetic values; their variance component is high, and this produces better prediction accuracy than the single-environment model (López-Cruz et al. 2015; Cuevas et al. 2016a). Environments with intermediate or high positive correlations indicate little GxE interaction. Thus, the model reacts by reducing the
specific marker effect. A correlation that is negative or close to zero implies strong G×E interaction, making it difficult to predict one environment based on information from another. With this, the model reduces the main effect of the marker, and increases the specific effects. To work around the limitations of the G×E models, Cuevas et al. (2016b) developed multi-environment Bayesian genomic models that allow an arbitrary genetic covariance structure between environments, because an unstructured covariance matrix was used, and its parameters were estimated from the data.

In this study, the prediction of multi-environment models was assessed by applying the CV strategy called CV2 in Burgueño et al. (2012) and (Cuevas et al. 2016a), where some lines are represented in some environments but not in others. This CV2 validation strategy performed better than CV strategy CV1 (where lines have not been evaluated in any field trials) proposed by Burgueño et al. (2012), when applied in multi-environment models (Jarquín et al. 2014; López-Cruz et al. 2015; Crossa et al. 2016b; Saint Pierre et al. 2016).

When introducing interaction effects, models MDs and the MDe showed increases in prediction accuracy for GY in most environments for the HEL and USP data sets over the single-environment model. Furthermore, models with GK had superior prediction accuracy than GB models. For traits PH and EH in both data sets, not much increase in prediction accuracy of MDs and MDe models was achieved over the single-environment model. These results were expected because the genetic architecture of traits PH and EH is less complex than that of GY and less influenced by environmental factors. When main marker effects and interaction effects are introduced in the model using covariance structures, this improves prediction accuracy.

The increase in accuracy when the interaction term for complex traits was included concurs with the findings of Crossa et al. (2016a), where increases in prediction accuracy were achieved by including dense molecular markers and G×E in a set of Mexican and Iranian landraces. Zhang et al. (2015) also used multi-environment models incorporating G×E, and obtained an increase in prediction accuracy of several maize biparental populations. Similarly, Saint Pierre et al. (2016) evaluated spring wheat lines and introduced other environmental covariates in the Jarquin’s model, showing that the prediction models gave better predictions using random CV. Recently, results of extensive analyses of spring wheat trials across international environments conducted for several years in South and West Asia, North Africa, and Mexico showed a consistent increase in the genomic prediction accuracy of the MDs-GB model over the MM-GB and SM-GB models (Sukumaran et al. 2017). One limitation of the data used in this study is that only 1 yr was available for assessing the genomic-enabled accuracy of the various models.

Our results show that predictions with medium-to-high accuracy for GS programs can be expected in environments with low-to-high heritability. Despite the low heritability of GY in P-LN and A-LN environments, the results were similar to results in other environments heritability. Despite the low heritability of GY in P-LN and A-LN environments, the results were similar to results in other environments heritability.

Conclusions
Incorporating the GK method into the model of Jarquin et al. (2014) increased prediction accuracy as compared to the model used with the linear kernel GBLUP; these results were found in both data sets with the models used in this study: MM across environments, MDs, and MDe.

Other results of the application of eight model-method combinations between four models (SM, MM, MDs, and MDe) and two kernel methods (GBLUP and Gaussian kernel) in two extensive maize data sets show that (1) genomic models incorporating G×E interaction had higher prediction accuracy than single-environment models; and (2) models with nonlinear Gaussian kernel had higher prediction accuracy than models with linear kernel GBLUP. The model-method combinations with the highest prediction accuracy were MDe-GK and MDs-GK. Results of this study indicated that by employing appropriate statistical genomic-enabled prediction models the researchers and plant breeders can improve the prediction of hybrids that were not evaluated in several environments. Random CV2 mimics sparse (incomplete) testing that allow to safe resources to the breeding program while improving prediction accuracy. Further research is required to compare the genomic-enabled G×E kernel prediction models used in this study with the models recently developed by Cuevas et al. (2016b), who studied genomic-enabled G×E models by means of Kronecker products applied to unstructured covariance matrices. It is also necessary to develop efficient computing software for fitting the structures considered in the models of this study while maintaining the inferential advantages of the Markov Chain Monte Carlo.

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APPENDIX A

In Box A1, we provide simplified scripts that can be used to obtain the GBLUP and GK matrix, to be used in the multi-environment models used in this study. The example uses the following R-object:
- X (n*p) a genomic marker matrix. The line IDs can be retrieved using either rownames(X) or SNP IDs in colnames(X).

Box A1. An Example of How to Obtain GBLUP (GB) and GK Matrix

```r
X<-scale(X,center=TRUE,scale=TRUE)
# G-BLUP kernel (GB)
GB<-tcrossprod(X)/ncol(X)
# Gaussian Kernel (GK)
dist<-as.matrix(dist(X))^2
GK<-exp(-dist/median(dist))
```

In the examples used to fit MM, MDs and MDe models, an R-object is necessary as matrix (pheno_geno) compound by three vectors of Location_id, Germplasm_id and Y, where:
- pheno_geno$Location_id vector is compound by environment information
- pheno_geno$Germplasm_id vector is compound by germplasm names
- pheno_geno$Y is a numeric and standardized vector with yield records in all environments

In Box A2 we give simplified scripts that can be used to fit models MM, MDs or MDe

Box A2. An Example of How to fit MDs model with cross-validation scheme CV2

```r
# Loading objects needed for MM, MDs and MDe models
library(BGLR)
env<-c(1,2,3,4) ### Choose environment
K<-GK #### Choose kernel GK or GB
model<-“MDs” ### Choose model “MM”or“MDs”or“MDe”
CV<-2 ### Choose CV=1 (CV1), CV=2 (CV2)
nEnv<-length(env)
pheno_geno1<-pheno_geno[pheno_geno$Location==env[1],]
i<-2
while (i <=nEnv){
pheno_geno1<-rbind(pheno_geno1,pheno_geno[pheno_geno$Location==env[i],])
i<-i+1
}
envID<-as.factor(pheno_geno1[,1])
IDs<-as.character(unique(pheno_geno1$Germplasm_id))
IDy<-pheno_geno1$Germplasm_id
Y<-as.numeric(pheno_geno1[,3])
Y<-scale(Y,center=TRUE,scale=TRUE)
names(Y)<-IDy
nEnv<-length(env)
K<-K[IDs,IDs]
phenol_geno1$Germplasm_id<-factor(x= phenol_geno1$Germplasm_id,levels=rownames(K),ordered=TRUE)
Zg <- model.matrix(~factor(phenol_geno1$Germplasm_id)-1) # genotype design matrix
Ze <- model.matrix(~factor(phenol_geno1$Location)-1) # environment design matrix
K1 <- Zg%K%*%t(Zg)
# CV scheme fit
```
set.seed(12345)
nFolds <- 5
partitions <- 10
if (CV == 1) {
mfold <- matrix(NA, ncol = partitions, nrow = length(IDs))
sets <- matrix(NA, nrow = nrow(phenogeno1), ncol = partitions)
for (s in 1:partitions) {
mfold[, s] <- sample(1:nFolds, size = length(IDs), replace = TRUE)
for (i in 1:nrow(phenogeno1)) {
sets[i, s] <- mfold[which(IDs == phenogeno1$Germplasm_id[i]), s]
}
}
if (CV == 2) {
sets <- matrix(NA, nrow = nrow(phenogeno1), ncol = partitions)
for (s in 1:partitions) {
for (i in IDs) {
tmp = which(IDy == i)
i = length(tmp)
tmpFold <- sample(1:nFolds, size = i, replace = i > nFolds)
sets[tmp, s] <- tmpFold
}
}
}
trn_tst <- matrix(nrow=nrow(phenogeno1),ncol=nFolds,NA)
NA.y <- matrix(Y, ncol = nFolds, nrow = length(Y))
# Fitting MM model
if (model == "MM") {
ETA <- list(ENV=list(X=Ze,model="FIXED"),
Grm=list(K=K1,model="RKHS"))
# Fitting MDs model
if (model == "MDs") {
ZEZE <- tcrossprod(Ze)
K2 <- K1*ZEZE
ETA <- list(ENV=list(X=Ze,model="FIXED"),
Grm=list(K=K1,model="RKHS"),
EGrm=list(K=K2,model="RKHS"))
# Fitting MDe model
if (model == "MDe") {
ETA <- list(ENV=list(X=Ze,model="FIXED"),
Grm=list(K=K1,model="RKHS"))
for(k in 1:nEnv){
ZEE <- matrix(0,nrow=nrow(Ze),ncol=ncol(Ze))
ZEE[,k] <- Ze[,k]
ZEEZ <- (ZEE%*%t(Ze))
K3 <- K1*ZEEZ
ETA[[k+2]] <- list(K=K3,model='RKHS')
}
COR <- matrix(0,nrow=nEnv,ncol=(nFolds*partitions))
for (s in 1:partitions) {
NA.y <- matrix(Y, ncol = (nFolds), nrow = length(Y))
for(i in 1:ncol(trn_tst)){
trn_tst[i,]<- ifelse(sets[i,]==i,"tst","trn")
NA.y[i][((trn_tst[i,]=="tst")]<-NA
A <- as.matrix(NA,y[,i])
fm <- BGLR(y=A,ETA=ETA,nIter=10000,burnIn=1000,thin=2)
for(g in 1:length(env)){
tst1 <- which(is.na(fm[y[envID==env[g]]]))
COR[g,((s-1)/nFolds+i)] <- cor(Y[envID==env[g]][tst1],fm$yHat[envID==env[g]][tst1])
}
}
}

APPENDIX B

Table B1 HEL data set

| Model/Environment | Multi-Environment, Main Genotypic Effect Model (MM) | Multi-environment, Main, Single Variance GxE Deviation Model (MDs) | Multi-Environment, Environment-Specific Variance GxE Deviation Model (MDe) |
|-------------------|---------------------------------------------------|-----------------------------------------------------------------|-------------------------------------------------|
|                   | GB       | GK       | % Change | GB       | GK       | % Change | GB       | GK       | % Change |
| Grain yield       |          |          |          |          |          |          |          |          |          |
| IP                | 0.48 (0.12) | 0.60 (0.08) | 25       | 0.65 (0.09) | 0.75 (0.05) | 15       | 0.64 (0.09) | 0.75 (0.05) | 17     |
| NM                | 0.36 (0.10) | 0.48 (0.09) | 33       | 0.41 (0.08) | 0.55 (0.07) | 34       | 0.41 (0.08) | 0.54 (0.07) | 32     |
| PM                | 0.60 (0.06) | 0.70 (0.05) | 17       | 0.68 (0.04) | 0.75 (0.04) | 10       | 0.68 (0.04) | 0.75 (0.04) | 10     |
| SE                | 0.17 (0.13) | 0.28 (0.11) | 65       | 0.32 (0.11) | 0.52 (0.08) | 63       | 0.31 (0.11) | 0.51 (0.09) | 65     |
| SO                | 0.27 (0.11) | 0.42 (0.10) | 56       | 0.39 (0.08) | 0.56 (0.07) | 44       | 0.38 (0.08) | 0.56 (0.07) | 47     |
| Plant height      |          |          |          |          |          |          |          |          |          |
| IP                | 0.72 (0.07) | 0.74 (0.06) | 3        | 0.73 (0.06) | 0.75 (0.06) | 3        | 0.73 (0.06) | 0.75 (0.06) | 3     |
| PM                | 0.75 (0.06) | 0.78 (0.05) | 4        | 0.76 (0.06) | 0.79 (0.05) | 4        | 0.76 (0.06) | 0.79 (0.05) | 4     |
| SE                | 0.74 (0.06) | 0.76 (0.05) | 3        | 0.75 (0.06) | 0.77 (0.05) | 3        | 0.75 (0.06) | 0.77 (0.05) | 3     |
| Ear height        |          |          |          |          |          |          |          |          |          |
| IP                | 0.71 (0.06) | 0.72 (0.06) | 1        | 0.72 (0.06) | 0.73 (0.06) | 1        | 0.72 (0.06) | 0.72 (0.06) | 0     |
| PM                | 0.74 (0.06) | 0.76 (0.06) | 3        | 0.76 (0.06) | 0.78 (0.05) | 3        | 0.76 (0.06) | 0.78 (0.05) | 3     |
| SE                | 0.72 (0.06) | 0.73 (0.05) | 1        | 0.72 (0.06) | 0.73 (0.05) | 1        | 0.72 (0.06) | 0.73 (0.05) | 1     |

Mean correlation (for 50 random partitions, CV1) for models multi-environment, main genotypic effect model GBLUP kernel (MM-GB), multi-environment, main genotypic effect GK (MM-GK), multi-environment, single variance GxE deviation model GBLUP kernel (MDs-GB), multi-environment, single variance GxE deviation model GK (MDs-GK), multi-environment, environment-specific variance GxE deviation model GBLUP kernel (MDe-GB), multi-environment, environment-specific variance GxE deviation model GK (MDe-GK) for three traits, grain yield, plant height, and ear height (SD in parentheses).

Environments: IP, Ipiacu; NM, Nova Mutum; PM, Pato de Minas; SE, Sertanopolis; and SO, Sorriso.
| Model/Environment | Multi-Environment, Main Genotypic Effect Model (MM) | Multi-Environment, Main Single Variance G\times E Deviation Model (MDs) | Multi-Environment, Environment-Specific Variance G\times E Deviation Model (MDe) |
|-------------------|-----------------------------------------------|-------------------------------------------------|-----------------------------------------------|
|                   | GB | GK | % Change | GB | GK | % Change | GB | GK | % Change |
| Grain yield       |    |    |          |    |    |          |    |    |          |
| P-LN              | 0.26 (0.06) | 0.27 (0.06) | 4 | 0.29 (0.07) | 0.29 (0.07) | 0 | 0.29 (0.07) | 0.28 (0.07) | −3 |
| P-IN              | 0.31 (0.07) | 0.30 (0.06) | −3 | 0.34 (0.07) | 0.33 (0.06) | −3 | 0.34 (0.07) | 0.33 (0.06) | −3 |
| A-LN              | 0.30 (0.08) | 0.28 (0.07) | −7 | 0.31 (0.07) | 0.27 (0.07) | −13 | 0.31 (0.07) | 0.28 (0.07) | −10 |
| A-IN              | 0.40 (0.06) | 0.39 (0.06) | −3 | 0.42 (0.05) | 0.41 (0.05) | −2 | 0.42 (0.05) | 0.41 (0.05) | −2 |
| Plant height      |    |    |          |    |    |          |    |    |          |
| P-LN              | 0.47 (0.06) | 0.45 (0.06) | −4 | 0.47 (0.06) | 0.44 (0.06) | −6 | 0.47 (0.06) | 0.44 (0.06) | −6 |
| P-IN              | 0.52 (0.06) | 0.48 (0.06) | −8 | 0.52 (0.06) | 0.49 (0.06) | −6 | 0.52 (0.06) | 0.49 (0.06) | −6 |
| A-LN              | 0.40 (0.07) | 0.41 (0.07) | 3 | 0.40 (0.07) | 0.40 (0.06) | 0 | 0.40 (0.07) | 0.40 (0.06) | 0 |
| A-IN              | 0.55 (0.05) | 0.51 (0.05) | −7 | 0.55 (0.05) | 0.52 (0.05) | −5 | 0.55 (0.05) | 0.52 (0.05) | −5 |
| Ear height        |    |    |          |    |    |          |    |    |          |
| P-LN              | 0.68 (0.04) | 0.67 (0.04) | −1 | 0.68 (0.04) | 0.67 (0.04) | −1 | 0.68 (0.04) | 0.66 (0.04) | −3 |
| P-IN              | 0.69 (0.04) | 0.68 (0.04) | −1 | 0.69 (0.04) | 0.68 (0.04) | −1 | 0.69 (0.04) | 0.68 (0.04) | −1 |
| A-LN              | 0.59 (0.06) | 0.59 (0.05) | 0 | 0.59 (0.06) | 0.58 (0.05) | −2 | 0.59 (0.06) | 0.58 (0.05) | −2 |
| A-IN              | 0.69 (0.03) | 0.68 (0.03) | −1 | 0.69 (0.03) | 0.68 (0.03) | −1 | 0.69 (0.03) | 0.68 (0.03) | −1 |

Mean correlation (for 50 random partitions, CV1) for models multi-environment, main genotypic effect model GBLUP kernel (MM-GB), multi-environment, main genotypic effect GK (MM-GK), multi-environment, single variance G\times E deviation model GBLUP kernel (MDs-GB), multi-environment, single variance G\times E deviation model GK (MDs-GK), multi-environment, environment-specific variance G\times E deviation model GBLUP kernel (MDe-GB), multi-environment, environment-specific variance G\times E deviation model GK (MDe-GK) for three traits, grain yield, plant height, and ear height (SD in parentheses).

\( ^a \) Environments: Anhumas ideal N (A-IN), Anhumas low N (A-LN), Piracicaba ideal N (P-IN) and Piracicaba low N (P-LN).