



The scale dependency of spatial crop species diversity and its relation to temporal diversity

Fernando Aramburu Merlos^{a,b,1} and Robert J. Hijmans^a

^aDepartment of Environmental Science and Policy, University of California, Davis, CA 95616; and ^bInstituto Nacional de Tecnología Agropecuaria, Unidad Integrada Balcarce, 7620 Balcarce, Buenos Aires, Argentina

Edited by Colin K. Khoury, International Center for Tropical Agriculture, Cali, Colombia, and accepted by Editorial Board Member Ruth DeFries August 21, 2020 (received for review June 7, 2020)

Increasing crop species diversity can enhance agricultural sustainability, but the scale dependency of the processes that shape diversity and of the effects of diversity on agroecosystems is insufficiently understood. We used 30 m spatial resolution crop classification data for the conterminous United States to analyze spatial and temporal crop species diversity and their relationship. We found that the US average temporal (crop rotation) diversity is 2.1 effective number of species and that a crop's average temporal diversity is lowest for common crops. Spatial diversity monotonically increases with the size of the unit of observation, and it is most strongly associated with temporal diversity when measured for areas of 100 to 400 ha, which is the typical US farm size. The association between diversity in space and time weakens as data are aggregated over larger areas because of the increasing diversity among farms, but at intermediate aggregation levels (counties) it is possible to estimate temporal diversity and farm-scale spatial diversity from aggregated spatial crop diversity data if the effect of beta diversity is considered. For larger areas, the diversity among farms is usually much greater than the diversity within them, and this needs to be considered when analyzing large-area crop diversity data. US agriculture is dominated by a few major annual crops (maize, soybean, wheat) that are mostly grown on fields with a very low temporal diversity. To increase crop species diversity, currently minor crops would have to increase in area at the expense of these major crops.

agrobiodiversity | temporal diversity | crop rotation | spatial scale

Variation in crop species diversity has been used to explain differences in the stability of food production (1), pesticide use (2), agroecosystem resilience (3), and natural biodiversity in agroecosystems (4–6). Recent analyses of aggregated data for large regions, such as counties and states in the United States, have shown both losses and gains in crop species diversity, depending on the location, the time period, and the level of spatial aggregation (7–11). It is not clear, however, how knowledge of changes over such large areas is related to agroecosystem function because our understanding of the effects of diversity on agroecosystems comes from studies on the scale of fields and landscapes (12–14). A more general understanding of the scale dependency of crop diversity patterns is therefore needed, as this could support the use of spatially aggregated data to study the effect of diversity in agriculture (15, 16). This is challenging conceptually (17) and practically because of the need for crop distribution data at a sufficiently high spatial resolution. There is also an important (short-term) temporal dimension of diversity that needs to be considered and can only be directly observed at a high spatial resolution: Many fields are planted in a seasonal sequence of multiple crops. These crop rotations can reduce pressure from pathogens, pest, and weeds (18–20) and improve soil quality (21), and it has been argued that these benefits are similar to those ascribed to spatial diversity in natural ecosystems (22), just as a rapid crop varietal turnover in time can compensate for genetic uniformity (13).

In this paper we use 30 m spatial resolution crop distribution data for the conterminous United States between 2008 and

2017 to show how crop species diversity changes with spatial scale. We also demonstrate that temporal diversity and farm-level spatial diversity can be estimated from aggregated spatial diversity data if the effect of spatial scale on diversity is taken into consideration.

Results

Temporal Crop Diversity. Average temporal crop species diversity ($D\tau$; the effective number of species) in the United States is 2.1. About 9% of the cropland has a single crop, 60% has two or fewer crops, and 86% has three or fewer crops in rotation (Fig. 1A). $D\tau$ is relatively high in large parts of North and South Dakota, along the Southern seaboard (from New Jersey to Georgia), in parts of the West Coast states and Idaho, and in northeast Michigan (Fig. 2 and *SI Appendix, Table S1*). Regions dominated by perennial crops, such as Florida and parts of California and Louisiana, have a $D\tau$ of 1, as expected. When not considering perennial crops (Fig. 2B), most areas in the West Coast states and Idaho have a high temporal diversity. Areas with monocropping of annual crops ($D\tau = 1$ in Fig. 2B) are predominant in Oklahoma (wheat), northern Texas (cotton), Montana (wheat), eastern Washington (wheat), and northern California (rice). Wheat has the largest monocrop area (2.9 Mha, 33% of all monocropped area), while 66% of the maize area (23 Mha) and 64% of the soybean area (20 Mha) have a temporal diversity of 2 (*SI Appendix, Table S2*).

The larger the area planted with a crop is, the lower the temporal diversity of the areas it is grown in is (Fig. 3). For annual crops that

Significance

There is considerable debate about the effect of changes in and the need to increase biodiversity in agriculture. The spatial scale dependency of crop diversity has not been formally addressed, and this complicates understanding and synthesis. Crop species diversity also has a temporal diversity component of fundamental importance that has been ignored in diversity assessments. To fill this gap, we develop a framework for understanding the scale dependency of spatial crop species diversity and its relation to temporal diversity using 30 m spatial resolution crop species distribution data for the United States. We show that aggregated diversity data can be downscaled to estimate spatial and temporal diversity at the farm scale. We use the results to discuss diversification strategies.

Author contributions: F.A.M. and R.J.H. designed research; F.A.M. performed research; F.A.M. analyzed data; and F.A.M. and R.J.H. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. C.K.K. is a guest editor invited by the Editorial Board.

Published under the PNAS license.

¹To whom correspondence may be addressed. Email: faramburumerlos@ucdavis.edu.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2011702117/-DCSupplemental>.

First published October 5, 2020.

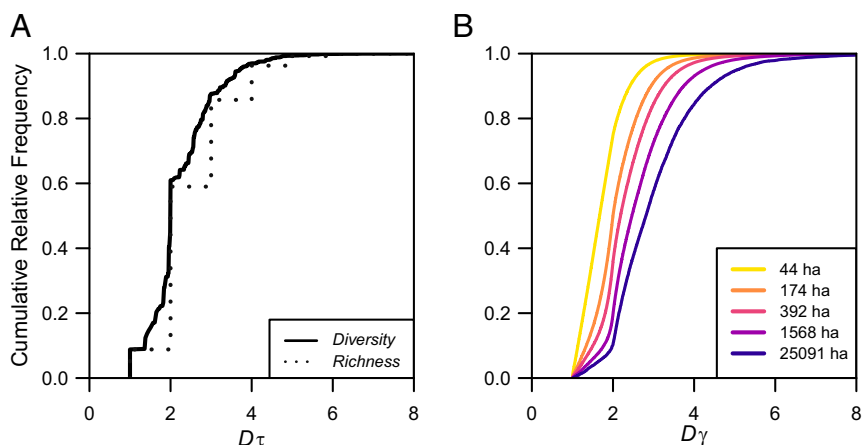


Fig. 1. Temporal (A, $D\tau$) and spatial (B, $D\gamma$) crop species diversity (effective number of crop species) in the conterminous United States for 2008 to 2017. Temporal diversity was computed at 30 m spatial resolution, and spatial diversity was computed at five different observational unit sizes. A also shows the temporal species richness (the number of different species, not accounting for their relative abundance).

cover at least 0.01% of the cropland area there is a strong log-linear decline of temporal diversity with crop area. For crops with less than 0.01% of the area, there is no clear effect of area planted, and $D\tau$ is about 3.7. The downward slope is expected because a crop that covers 100% of an area can only have $D\tau = 1$, and an area with two crops that each cover 50% can only have $D\tau \leq 2$. But the empirical data are far below this theoretical maximum. The fields

with the highest temporal diversity ($D\tau \geq 4$) are mostly planted with crops grown for fresh consumption such as eggplants, lettuce, and carrots.

Spatial Crop Diversity. Spatial crop species diversity ($D\gamma$) strongly increases with the size of the observational unit (Figs. 1, 4, and 5). When measured on areas of 44 ha, only 25% of US cropland has a $D\gamma \geq 2$ (that is, two equally abundant crops or more), and 2.5% of the cropland has a $D\gamma \geq 3$ (Figs. 1 and 4A). In contrast, 80% of the cropland has a $D\gamma \geq 2$ when the observational unit is 1,568 ha, and this increases to 90% for units of 25,091 ha (Figs. 1 and 4D). Spatial diversity patterns are highly apparent at this level of aggregation, showing large tracts of low spatial crop species diversity in Florida, southern Louisiana, northern Texas, Oklahoma, and parts of Montana and Washington (Fig. 4D). $D\gamma$ is also low in isolated croplands in western regions where alfalfa is grown in areas dominated by rangelands (SI Appendix, Fig. S1). Most of the Corn Belt (and Nebraska) has $D\gamma \sim 2$. Kansas and the Mississippi Portal (the southern half of the Mississippi basin) have $D\gamma \sim 3$, while the regions with the highest $D\gamma (\geq 4)$ are found along the coasts and borders with Canada and Mexico.

Country-wide average $D\gamma$ monotonically increases as diversity is computed over larger areas (Fig. 5A). $D\gamma$ increases exponentially as it moves away from fields (with generally only one crop at a time) to multiple fields and captures more of the farm-level diversity. When the observational units reach about 400 ha, the increase in $D\gamma$ slows down as neighboring farms are generally similar to each other. $D\gamma$ then increases exponentially again at very large areas (>1 Mha), reaching 5.4 at 411 Mha (Fig. 5A) and 8.1 at the national level.

The average regional-to-local diversity ratio, $D\beta$ (always computed with 392 ha subunits to have a constant definition of “local”), remains low and close to 1 (that is, no difference in diversity) as the regional area increases in size, until the regions considered are as about as big as a state, at which point it increases exponentially (SI Appendix, Fig. S2). This again shows that crops grown on different farms tend to be similar at the county to state level but not across larger areas. At observational units of intermediate size, such as 25,091 ha, crop species diversity is most strongly associated with farm-level diversity, represented here by $D\alpha$ (local diversity) with 392 ha subunits. For instance, if the United States is divided in square regions of 0.4 Mha (that is, comparable to the size of a county), only a few regions have $D\beta \geq 2$, including parts of California, western South and North Dakota, eastern Montana, and Washington

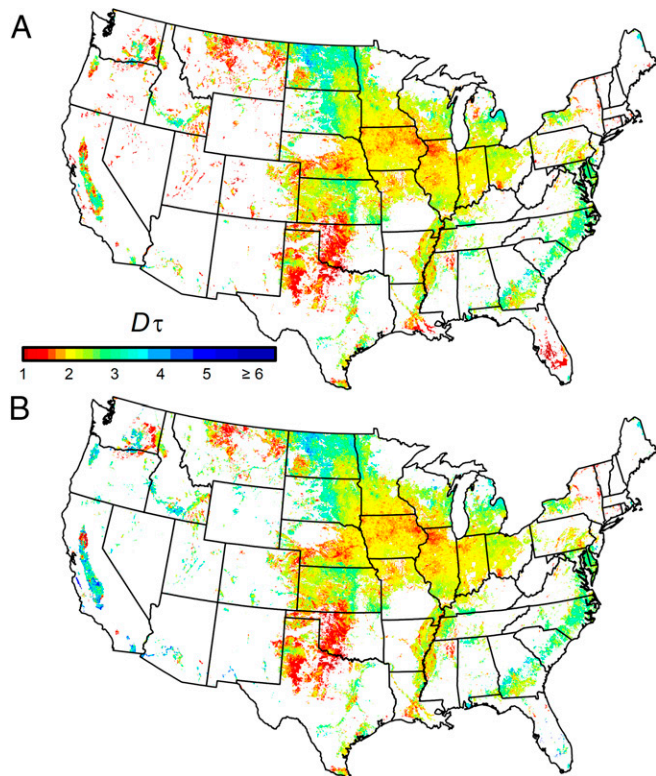


Fig. 2. Temporal crop species diversity ($D\tau$) in the conterminous United States (2008 to 2017) measured as the effective number of crops species in rotation considering (A) all crop species and (B) only annual crops. $D\tau$ was computed at a 30 m resolution and then aggregated to a 3.96 km resolution for display purposes. Aggregated cells with less than 10% of cropland were not considered. In B, 30 m cells classified as perennial crops in four or more years were removed from the calculation of average $D\tau$ for the aggregated cells.

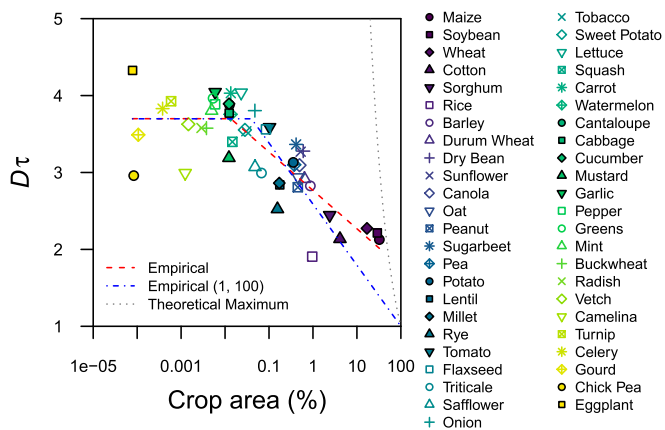


Fig. 3. Mean temporal crop species diversity ($D\tau$, effective number of crop species) by crop as a function of their area planted (percentage of cropland) for annual crops in the conterminous United States. The means are for all 30 m spatial resolution cells in which a crop occurred between 2008 and 2017. The horizontal axis has a logarithmic scale. The red dashed line is a fitted log-linear regression line: $D\tau = \min(3.699; 1.769 - 0.499 \log(\text{area}))$, where area is the area planted as a proportion of total cropland. The blue dot-dashed line is a fitted log-linear regression line forced through (1, 100): $D\tau = \min(3.698; 1 - 0.794 \log(\text{area}))$. The gray dotted line represents the theoretical maximum for a situation in which all crops are in equal area and grown everywhere with the same frequency, $D\tau = 1/\text{area}$.

(SI Appendix, Fig. S3). But $D\alpha$ is still greater than $D\beta$ in most of these regions.

Association between Spatial and Temporal Crop Species Diversity.

The relation between spatial and temporal crop species diversity depends on the size of the observational unit of analysis, and it is strongest between 100 and 400 ha (Fig. 5B), which is about the size of a typical US farm (23). If spatial diversity is measured on smaller areas (<100 ha), $D\tau$ tends to be greater than $D\gamma$, while the opposite occurs at larger areas (>400 ha) (Fig. 5A). Consider the extreme cases: If the spatial diversity were measured at a point (an infinitesimal small area), $D\gamma$ would always be 1 because only one crop could be present, but $D\tau$ would change from place

to place depending on the crop rotation of each site, so no association would exist. At the other extreme, national $D\gamma$ is 8.1, almost four times the national average $D\tau$ of 2.1.

The smallest root-mean-square deviation (RMSD) between $D\tau$ with $D\gamma$ is that measured on areas of 174 ha, although it barely changes in the range of 100 to 400 ha (Fig. 5B). The lowest lack of correlation (and greatest correlation) between $D\tau$ and $D\gamma$ is at an area of 1,568 ha, probably because averaging larger areas reduces noise stemming from variation in field sizes, cropland fraction per observational unit, noise in the data, and other factors. At higher levels of aggregation, however, the lack of correlation rapidly escalates beyond 1 because of the increasingly strong influence of $D\beta$ on $D\gamma$ (SI Appendix, Fig. S2). At the county level, $D\gamma$ is always greater than or equal to average county $D\tau$, and the difference between these two measures is associated with the number of crop species assemblages (cropping systems with different species composition) in each county, measured by $D\beta$ (Fig. 6A). Strong agreement between spatial and temporal diversity at the county level is achieved when $D\beta$ is removed from $D\gamma$ by applying the equality in Eq. 3, ensuring that $D\alpha$ (that is, 174 ha subunit diversity averages, a proxy for farm-level diversity) is properly considered (Fig. 6B).

Discussion

We have analyzed the variation in temporal and spatial crop species diversity in the United States and have shown how these are related. Spatial diversity is most strongly associated with temporal diversity at the farm level. For county to state-sized regions, the total spatial diversity is mainly determined by farm-level diversity, and the diversity among farms at this level of aggregation is low. At the national level, in contrast, the variation among farms and regions is much greater than within them. Understanding the effect of scale on diversity is important because both the processes shaping diversity and the effects of diversity on ecosystem functioning vary with scale. Our analytical approach could be applied to research on other levels of agricultural biodiversity, such as genetic diversity within species (16) and contexts (6, 24), which would also benefit from more formal conceptual frameworks for the analysis of spatial scale.

Our analysis of the scale dependency in crop species diversity allows for improved comparison between regions and countries.

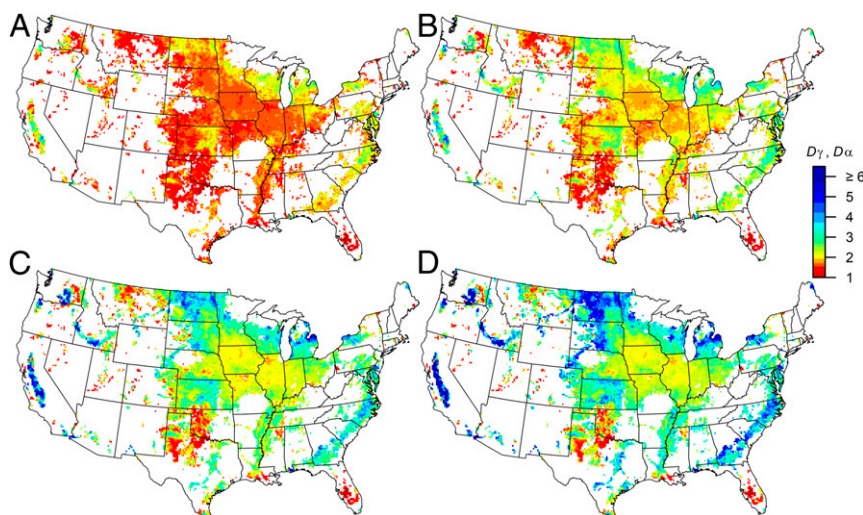


Fig. 4. Spatial crop species diversity (effective number of crop species) in the conterminous United States (2008 to 2017) at four observational unit sizes: (A) 44 ha, (B) 174 ha, (C) 1,568 ha, and (D) 25,091 ha (15.84 km resolution). For comparison, all maps are displayed at a 15.84 km resolution, and smaller units' results were aggregated by computing their weighted average value using Eq. 2. In D, the diversity is the total diversity of each 15.84 km grid cell ($D\gamma$), whereas on the other maps, each grid cell shows the mean effective number of crop species for subunits at the corresponding spatial scale ($D\alpha$). Only cells with more than 5% of crop area are included.

Downloaded from https://www.pnas.org by UNIV OF NE-LINCOLN LIBRARIES on July 21, 2022 from IP address 129.93.161.223.

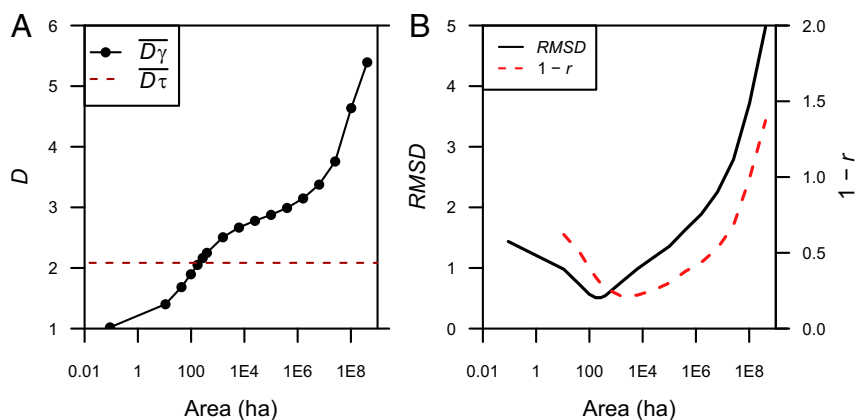


Fig. 5. Scale dependency of spatial crop species diversity and its association with temporal diversity. (A) Average crop species diversity (effective number of crop species) in space ($\overline{D_\gamma}$) and time ($\overline{D_\tau}$) for the conterminous United States (2008 to 2017) at different observational unit sizes. (B) Summary statistics for the difference between D_γ and D_τ as a function of the size of the observational unit. Here, RMSD is the root-mean-squared deviation and $1 - r$ is the lack of positive correlation, where r is Pearson's correlation coefficient. In both plots the horizontal axis has a logarithmic scale.

Departures from the relationship between crop diversity and spatial aggregation level that we described should reflect differences in temporal diversity and/or farm (and field) sizes. Regions with smaller farms and fields would present a first inflection point at smaller areas, while those with more diverse rotations would have it at higher diversity values. Similarly, the second exponential growth phase depends on how different the farms are from each other as larger areas are considered. Data for countries with greater diversity among cropping systems than the United States, perhaps because of greater environmental diversity, would show a steeper increase and reach a higher level. Variation in the relationship between crop dominance and temporal diversity, notably the location of the inflection point and the slope, should also allow for a more quantitative understanding of crop diversity patterns.

Temporal diversity (crop rotation) has been studied in the context of the multiple agronomic benefits it provides (25–29), but farm-level temporal diversity assessments are rare. Our study formally analyzes temporal crop diversity patterns over a large area. It is important to distinguish “temporal diversity” from “changes in spatial diversity over time” (30), which has been used in prior work (6–8). True temporal diversity is a key system property of croplands. There is also temporal diversity in natural ecosystems, which may merit more formal evaluation. For example, the temporal diversity concept might be useful for understanding the role of biodiversity in ecosystems with short-term (fire-driven) succession (31) or variation in species distributions and abundance driven by cycles in ocean temperature (32), masting (33), and annual migration.

Monitoring changes over time in temporal diversity in agriculture is important (34–37), but it requires time series of high spatial resolution crop distribution data that generally do not exist. While the increasing availability of remote sensing-derived cropland classification data will enable future study of temporal crop diversity, we need methods to assess historical changes in temporal crop diversity. Our results suggest that we can do so by using the tight association of temporal and spatial crop diversity for areas close to the median farm size. In the United States, that is between 100 and 400 ha. We have shown that with observational units of that size, temporal crop diversity can be predicted from a single year of high spatial resolution data. If temporal diversity needs to be predicted from more aggregated data, the effective number of cropping system types (D_β) must be considered in order to avoid overestimation. This method should be reliable at intermediate levels of aggregation (such as counties in

the United States), but it should be used with great caution with more aggregated data since the lack of correlation between spatial and temporal diversities increases exponentially as data are aggregated over larger areas. Future work could investigate this further using, for example, environmental dissimilarity to predict cropping system variability within large regions.

A compelling case has been made for increasing the diversity of cropping systems (1, 5, 6, 38–41), and our analysis can help us to understand some important aspects that need to be considered. Minor annual crops tend to be grown in more diverse rotations than major crops. However, minor crops cover, by definition, only a small area. In addition, minor crops are often restricted to specific regions, in part because of favorable environmental conditions and in part because of regional specialization leading to the presence of superior infrastructure for processing and distribution (42). In contrast, major crops are sometimes the only profitable option. For instance, wheat might be the only cost-effective crop in the United States in cold or dry environments (43). Moreover, changes in relative crop prices that favor major crops, such as those caused by an increasing bioethanol demand, have been shown to negatively affect diversity (12). A better understanding of the drivers of crop spatial distribution, crop price

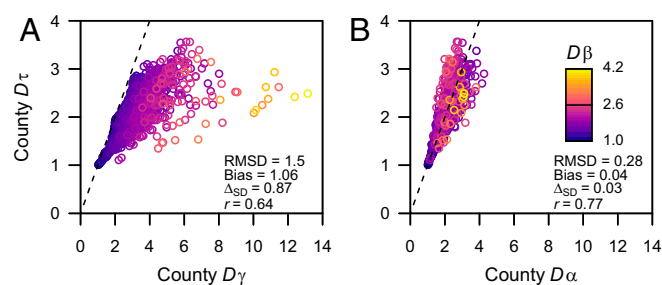


Fig. 6. County-level average temporal crop species diversity (D_τ) in the conterminous United States as a function of two spatial diversity measurements. (A) County-level spatial diversity (D_γ) and (B) subunit average (174 ha) crop species diversity (D_α) for each county. The color of each point indicates the region-to-local diversity ratio (D_β) for each county based on 174 ha subunits. The same color ramp was used for both plots and is shown in B. For both plots, the dashed line represents the identity function ($D_\tau = D_\gamma$). The root-mean-squared deviation (RMSD), mean bias, difference between standard deviations (Δ_{SD}), and Pearson's correlation coefficient (r) for the agreement between D_τ and the corresponding spatial diversity type are shown on each plot. Only counties with more than 5% of crop area are included.

effects, and why certain crops present greater temporal diversity than others should inform opportunities for and constraints on the development of more diverse cropping systems.

National-level diversity in the United States is quite low. Despite its large size and wide range of environmental conditions, the United States is in the 29th percentile when comparing country-level crop diversity globally (11). We found that farm-scale diversity is also low in most of the country, in large part because of the great predominance of three major crops. Wheat, maize, and soybean crops cover most of the US cropland, and despite the hundreds of other crops that are grown in the United States, it is not possible to create much more diverse cropping systems unless the area planted with these three dominant commodities decreases drastically. This would require major changes in the food system that would be rather costly in the short term (44). Our analysis suggests that an important approach to increasing farm-scale crop diversity is to provide financial incentives and improved technology for the production of smaller crops such that it becomes more attractive to bring them into rotation with maize, soybean, and/or wheat. This is what the United States looked like in the 1950s when there was a much larger “middle class” of crops, including barley, oats, and sorghum (8). It could also be relevant to consider how to get more variability among neighboring farms, as we showed that this tends to be very low. An increased emphasis on consumption of locally produced fresh food (45) could perhaps play a modest role. Reintegration of crop production and livestock production, that is, with local sourcing of feed, could diversify farms and greatly reduce environmental pollution stemming from concentrated livestock production as well (39, 46). Cover crops constitute another diversification strategy that has gained popularity in recent years, particularly in areas with poor soils and long growing seasons (47). These crops planted to protect the soil and/or avoid leaching of nutrients may provide larger ecosystem services than adding another crop planted for its harvestable product (48).

Acknowledging the scale dependency of spatial diversity and the role of diversity in time is critical for the analysis of diversification strategies and their effects. While both human health and the environment would benefit from more diverse diets and food production (49–51), we must assess how to deploy current crops in space and time. Many authors advocate for high diversity at the field level (38, 52–54), but field-level diversification benefits are context dependent. For instance, intercrops (in-field mixtures of annual crops) are most commonly used in N-deprived systems of developing countries (55), where legume–cereal mixes provide a clear advantage over the monocrop alternatives (56), or when they provide temporal complementarity (57), resembling a crop rotation. However, intercrops are rarely compared against their temporal diversification alternative (22). Temporal diversity allows for greater field-level diversity without running into the practical management problems of intercrops. Furthermore, temporal diversity might be better for the control of soilborne pests and disease (58) and for other ecosystem services as well (27, 59). Diverse crop rotations also foster farm-level spatial diversity, as farmers tend to cultivate all crop rotation components every year, but how this shapes the landscape and its effects on ecosystem services depends on field and farm sizes. For instance, natural biodiversity associated with agriculture increases when the landscape is composed of small fields (<6 ha) and a diverse mosaic of crops (5). This composite of small and diverse fields implies high spatial diversity even when measured on units of 44 ha. In most of the United States, however, diversity is very low at this level because of the combination of large fields (60, 61) and low temporal diversity. Even the most diverse regions of the United States present a relatively low diversity when considering observational units of 392 ha or smaller.

Beyond farms and landscapes, national-level crop diversity has been associated with food production stability (1). While there

can be benefits to high crop diversity at the national level, this is different from having high crop diversity at the farm and landscape levels. We showed that the diversity among cropping systems ($D\beta$) can be a far greater determinant of national-level diversity than the diversity within them ($D\alpha$) because $D\beta$ increases exponentially at higher aggregation levels. $D\beta$ might also have a stronger stability effect on national food production than $D\alpha$ because yields of different cropping systems and regions are usually less correlated among each other than yields within the same cropping system (62). Therefore, identifying the role of $D\alpha$ and $D\beta$ on the diversity–stability relation is necessary in order to better understand the relation between crop diversity and food production stability at the farm level. Downscaling spatial diversity to farm level by removing the effect of $D\beta$ would allow for using average farm-level diversity, which is likely a more relevant measure when investigating the relation between crop diversity and other agroecosystem properties.

Materials and Methods

Data Source and Preparation. We used the Cropland Data Layers (CDLs) annual crop-specific land cover classifications for the conterminous United States (63, 64). Each CDL has a spatial resolution of 30 m and classifies each raster cell as cropland or not and each cropland cell as 1 of 106 crop classes, which can either be a single crop or a double crop (e.g., winter wheat/soybean). We used the 10 years of CDLs (from 2008 to 2017) that were available at the beginning of this project. Early CDL years have been reprocessed and rereleased, bringing them to a similar level of accuracy as later years (Cohen’s kappa coefficient ~ 0.83), which constitutes a significant improvement for our multiyear analyses. The typical crop field in the United States ranges between 16 and 65 ha (61), much larger than the CDL spatial resolution (0.09 ha), and the CDL data have been used to study changes in crop rotations (34–37), suggesting that the CDLs provide high enough spatial and temporal resolution to assess temporal diversity. CDL-derived spatial diversity estimates at the county level and those obtained based on the US Department of Agriculture Census of Agriculture showed strong agreement between both datasets (root-mean-square error (RMSE) = 3% of Shannon entropy index average, *SI Appendix*, Fig. S4).

We aggregated CDL classes by species. For example, corn, sweet corn, popcorn, and ornamental corn were grouped as maize (*SI Appendix*, Table S3). Each double-crop type remained as a different category, and both species within the double crop were fully considered for the calculation of spatial and temporal crop diversity. Only land that was classified as cropland for more than 5 years was considered. That threshold was chosen for two reasons: 1) to avoid the influence of areas cropped only for a few years on temporal diversity estimations and 2) as a data-cleaning process since most land that is only occasionally classified as cropland is probably never used for that purpose.

Spatial and Temporal Diversity. We follow the definition and partition of diversity proposed by Jost (65) and reviewed by Tuomisto (66). A true diversity (D) quantifies the effective number of types of entities, which in this case refers to crop species. The effective number of crop species in space (D_Y) or time (D_T) is the number of equally abundant virtual crop species that has the same entropy as the actual crop species given their mean relative abundance. D is calculated as an exponent of the Shannon entropy index (H) (65, 66):

$$D = \exp\left(-\sum_{i=1}^S (p_i \ln p_i)\right) = \exp(H), \quad [1]$$

where p_i is the proportion of cropland area covered with crop species i and S is the number of crop species.

We computed D_Y for square grid cells of different spatial resolutions covering the conterminous United States. A grid cell represents an observational unit, which can have different sizes according to the spatial resolution. The median crop field size in the United States considering the fraction of cropland area is 35 ha (61), and the median farm size is 445 ha (23). We used a series of spatial resolutions that were aggregates of the original 30 m grid cells, selecting six resolutions at field to farm scales (from 0.33 to 1.98 km in steps of 0.33 km) and an additional 10 resolutions by increasing the cell sizes exponentially by multiplying 0.99 km with 2^x (in which x can take any integer value between 2 and 11), that is, a sequence of resolutions of 0.33, 0.66, 0.99, 1.32, 1.65, 1.98, 3.96, 7.92, 15.8, 31.7, 63.4, 127, 253, 507, 1,014, and 2,028 km, which yields observational units of 11, 44, 98, 174, 272, 392, 1,568, 6,273, 25,091, 0.1×10^6 , 0.4×10^6 , 1.6×10^6 , 6.4×10^6 , 26×10^6 , 103×10^6 , and 411×10^6 ha.

When an observational unit is divided into smaller subunits, its total ("regional") spatial diversity, D_γ , can be partitioned into its α and β components (67), with D_α referring to the local diversity and D_β referring to the regional-to-local diversity ratio. Both components depend on the definition of "local," which might be set by the aggregation level of the input data (e.g., farm, county, or state data) or might be arbitrarily selected if higher-resolution data are available. Here, for all observational units with an area greater than or equal to 1,568 ha, their total diversity (D_γ) was partitioned into D_α (local diversity) and D_β (regional-to-local diversity ratio) by applying Eqs. 2 and 3 and using all grids with smaller cells whose borders perfectly fit within the observational units (in other words, the division between resolutions is without remainder). For example, the 15.84 km resolution grid was partitioned using the 0.33, 0.66, 0.99, 1.32, 1.98, and 3.96 km cells as subunits, and different α and β diversities estimations were obtained for all those subunit sizes:

$$D_\alpha = \exp \left[- \sum_{j=1}^N \left(w_j \sum_{i=1}^S (p_{ij} \ln p_{ij}) \right) \right], \quad [2]$$

$$D_\beta = D_\gamma / D_\alpha. \quad [3]$$

In Eq. 2, N is the number of subunits in a given area, and w_j is the weight of subunit j , estimated as the number of cropland pixels within the subunit divided by the total number of cropland pixels in that area. D_α is thus the weighted mean effective number of crop species of the subunits, while D_β expresses how many times as diverse the observational unit is compared with the average diversity of its subunits (66).

Temporal crop species diversity (D_τ) was calculated with 10 years of data (2008 to 2017) with Eq. 1 at a 30 m spatial resolution and then aggregated to the same resolutions used for D_γ by applying Eq. 4 in order to maintain an equivalent relation between spatial and temporal diversity:

$$D_{\tau(r)} = \exp \left(\frac{\sum_{i=1}^n \ln D_{\tau(30)}}{n} \right). \quad [4]$$

In Eq. 4, n is the number of 30 m cropland grid cells for a cell at resolution r . In other words, instead of averaging temporal diversity values at 30 m resolution, D_τ (at the resolution r) is computed as the exponent of the average of the Shannon index for temporal crop diversity. Accordingly, 10 year

averages of D_γ , D_α , and D_β were computed as the exponent of the weighted average of the Shannon index of each year in order to ensure the equality in Eq. 3 at all levels of aggregation. Back transforming diversities to the Shannon index when averaging and aggregating to other resolutions is necessary because entropies have better mathematical properties than diversities (which also happens with coefficients of variation compared to standard deviations), and it would be wrong to simply average diversity values (65).

Postprocessing and Analysis. Diversity estimates based on very low crop area have greater uncertainty and, on average, lower diversity values. For that reason, observational units with a crop area lower than certain thresholds were removed from analysis. These thresholds ranged from 11 to 0.5% (lower percentages for larger observational unit sizes) and were defined, for each resolution, as the crop area in which the last segment of a two-piece linear spline of D_γ as a function of crop area (%) no longer yields a significant positive slope ($P > 0.01$; *SI Appendix, Fig. S5*).

Then, D_γ , D_τ , D_α , and D_β within the conterminous United States were mapped, and correlations among different levels and types of crop species diversities were assessed in order to examine the association between the spatial and temporal dimensions of crop species diversity. We measured the level of (dis)agreement between D_γ and D_τ at different aggregation

levels with the root-mean-square deviation ($\text{RMSD} = \sqrt{\frac{1}{n} \sum_1^n (D_{\gamma_i} - D_{\tau_i})^2}$) and

its components: bias ($\text{Bias} = \overline{D_\gamma} - \overline{D_\tau}$), the difference between population standard deviations ($\Delta_{SD} = SD_{D_\gamma} - SD_{D_\tau}$), and the lack of positive correlation ($1 - r$, where r is Pearson's correlation coefficient). Note that $\text{RMSD}^2 = \text{Bias}^2 + \Delta_{SD}^2 + (2 \times SD_{D_\gamma} \times SD_{D_\tau} \times (1 - r))$ (68). We evaluated how county-level spatial diversity relates to county average D_τ . We compared the agreement between county D_τ averages and 1) county D_γ and 2) county D_α based on 174 ha subunits.

All data analysis was done with R (69), and the scripts used for this study are available at https://github.com/AramburuMerlos/cropdiv_usa.

Data Availability. All study data are included in the article and *SI Appendix*.

ACKNOWLEDGMENTS. F.A.M. was supported by the Fulbright Program and the Argentine Ministry of Education.

- D. Renard, D. Tilman, National food production stabilized by crop diversity. *Nature* **571**, 257–260 (2019).
- A. E. Larsen, F. Noack, Identifying the landscape drivers of agricultural insecticide use leveraging evidence from 100,000 fields. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 5473–5478 (2017).
- A. C. Gaudin *et al.*, Increasing crop diversity mitigates weather variations and improves yield stability. *PLoS One* **10**, e0113261 (2015).
- C. Kremen, A. M. Merenlender, Landscapes that work for biodiversity and people. *Science* **362**, eaau6020 (2018).
- C. Sirami *et al.*, Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 16442–16447 (2019).
- I. Perfecto, J. Vandermeer, The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 5786–5791 (2010).
- J. Aguilar *et al.*, Crop species diversity changes in the United States: 1978–2012. *PLoS One* **10**, e0136580 (2015).
- R. J. Hijmans, H. Choe, J. Perlman, Spatiotemporal patterns of field crop diversity in the United States, 1870–2012. *Agric. Environ. Lett.* **1**, 160022 (2016).
- D. Renard, E. M. Bennett, J. M. Rhemtulla, Agro-biodiversity has increased over a 95 year period at sub-regional and regional scales in southern Quebec, Canada. *Environ. Res. Lett.* **11**, 124024 (2016).
- J. C. Smith, A. Ghosh, R. J. Hijmans, Agricultural intensification was associated with crop diversification in India (1947–2014). *PLoS One* **14**, e0225555 (2019).
- M. A. Aizen *et al.*, Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Glob. Chang. Biol.* **25**, 3516–3527 (2019).
- D. A. Landis, M. M. Gardiner, W. van der Werf, S. M. Swinton, Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 20552–20557 (2008).
- M. J. Swift, A.-M. Izac, M. van Noordwijk, Biodiversity and ecosystem services in agricultural landscapes—Are we asking the right questions? *Agric. Ecosyst. Environ.* **104**, 113–134 (2004).
- T. Tschamtké, A. M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies, Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol. Lett.* **8**, 857–874 (2005).
- B. B. Lin, Resilience in agriculture through crop diversification: Adaptive management for environmental change. *Bioscience* **61**, 183–193 (2011).
- K. L. Mercer *et al.*, "Crop evolutionary agroecology: Genetic and functional dimensions of agrobiodiversity and associated knowledge" in *Agrobiodiversity: Integrating Knowledge for a Sustainable Future*, K. S. Zimmerer, S. de Haan, Eds. (Strüngmann Forum Reports, MIT Press, 2019), pp. 20–62.
- S. A. Levin, The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology* **73**, 1943–1967 (1992).
- D. G. Bullock, Crop rotation. *Crit. Rev. Plant Sci.* **11**, 309–326 (1992).
- E. A. Curl, Control of plant diseases by crop rotation. *Bot. Rev.* **29**, 413–479 (1963).
- M. Liebman, E. Dyck, Crop rotation and intercropping strategies for weed management. *Ecol. Appl.* **3**, 92–122 (1993).
- L. K. Tiemann, A. S. Grandy, E. E. Atkinson, E. Marin-Spiotta, M. D. McDaniel, Crop rotational diversity enhances belowground communities and functions in an agroecosystem. *Ecol. Lett.* **18**, 761–771 (2015).
- R. F. Denison, *Darwinian Agriculture: How Understanding Evolution Can Improve Agriculture* (Princeton University Press, 2012).
- J. M. MacDonald, P. Korb, R. A. Hoppe, *Farm Size and the Organization of US Crop Farming* (US Department of Agriculture Economic Research Service, Washington, DC, 2013).
- S. A. Wood *et al.*, Functional traits in agriculture: Agrobiodiversity and ecosystem services. *Trends Ecol. Evol.* **30**, 531–539 (2015).
- J. M. Krupinsky, K. L. Bailey, M. P. McMullen, B. D. Gossen, T. K. Turkington, Managing plant disease risk in diversified cropping systems. *Agron. J.* **94**, 198–209 (2002).
- M. Liebman *et al.*, Ecologically sustainable weed management: How do we get from proof-of-concept to adoption? *Ecol. Appl.* **26**, 1352–1369 (2016).
- M. D. McDaniel, L. K. Tiemann, A. S. Grandy, Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecol. Appl.* **24**, 560–570 (2014).
- L. L. Renwick, T. M. Bowles, W. Deen, A. C. Gaudin, "Potential of increased temporal crop diversity to improve resource use efficiencies: Exploiting water and nitrogen linkages" in *Agroecosystem Diversity*, G. Lemaire, P. C. de Faccio Carvalho, S. Kronberg, S. Recous, Eds. (Elsevier, 2019), pp. 55–73.
- G. A. Studdert, H. E. Echeverria, Crop rotations and nitrogen fertilization to manage soil organic carbon dynamics. *Soil Sci. Soc. Am. J.* **64**, 1496–1503 (2000).
- M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge University Press, 1995).
- M. I. Shafi, G. A. Yarranton, Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology* **54**, 897–902 (1973).

32. J. A. Santora *et al.*, Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem. *Mar. Ecol. Prog. Ser.* **580**, 205–220 (2017).
33. W. D. Koenig, J. M. H. Knops, The mystery of masting in trees: Some trees reproduce synchronously over large areas, with widespread ecological effects, but how and why? *Am. Sci.* **93**, 340–347 (2005).
34. J. Ren, J. B. Campbell, Y. Shao, Spatial and temporal dimensions of agricultural land use changes, 2001–2012, east-central Iowa. *Agric. Syst.* **148**, 149–158 (2016).
35. C. A. Seifert, M. J. Roberts, D. B. Lobell, Continuous corn and soybean yield penalties across hundreds of thousands of fields. *Agron. J.* **109**, 541–548 (2017).
36. J. D. Plourde, B. C. Pijanowski, B. K. Pekin, Evidence for increased monoculture cropping in the central United States. *Agric. Ecosyst. Environ.* **165**, 50–59 (2013).
37. A. Stern, P. C. Doraiswamy, E. R. Hunt, Changes of crop rotation in Iowa determined from the United States Department of Agriculture, National Agricultural Statistics Service Cropland Data Layer product. *J. Appl. Remote Sens.* **6**, 063590 (2012).
38. C. Kremen, A. Iles, C. Bacon, Diversified farming systems: An agroecological, systems-based alternative to modern industrial agriculture. *Ecol. Soc.* **17**, 44 (2012).
39. G. Lemaire, P. C. de Faccio Carvalho, S. Kronberg, S. Recous, *Agroecosystem Diversity: Reconciling Contemporary Agriculture and Environmental Quality* (Academic Press, 2018).
40. J. Pretty *et al.*, Global assessment of agricultural system redesign for sustainable intensification. *Nat. Sustain.* **1**, 441–446 (2018).
41. S. Spiegel *et al.*, Evaluating strategies for sustainable intensification of US agriculture through the Long-Term Agroecosystem Research Network. *Environ. Res. Lett.* **13**, 034031 (2018).
42. G. E. Roesch-McNally, J. G. Ar buckle, J. C. Tyndall, Barriers to implementing climate resilient agricultural strategies: The case of crop diversification in the US Corn Belt. *Glob. Environ. Chang.* **48**, 206–215 (2018).
43. E. G. Smith, R. P. Zentner, C. A. Campbell, R. Lemke, K. Brandt, Long-term crop rotation effects on production, grain quality, profitability, and risk in the Northern Great Plains. *Agron. J.* **109**, 957–967 (2017).
44. R. Trostle, *Global Agricultural Supply and Demand: Factors Contributing to the Recent Increase in Food Commodity Prices* (DIANE Publishing, rev. ed., 2010).
45. G. Berti, C. Mulligan, Competitiveness of small farms and innovative food supply chains: The role of food hubs in creating sustainable regional and local food systems. *Sustainability* **8**, 616 (2016).
46. G. Lemaire, F. Gastal, A. Franzluebbers, A. Chabbi, Grassland-cropping rotations: An avenue for agricultural diversification to reconcile high production with environmental quality. *Environ. Manage.* **56**, 1065–1077 (2015).
47. C. A. Seifert, G. Azzari, D. B. Lobell, Satellite detection of cover crops and their effects on crop yield in the midwestern United States. *Environ. Res. Lett.* **13**, 064033 (2018).
48. H. Blanco-Canqui *et al.*, Cover crops and ecosystem services: Insights from studies in temperate soils. *Agron. J.* **107**, 2449–2474 (2015).
49. D. Tilman, M. Clark, Global diets link environmental sustainability and human health. *Nature* **515**, 518–522 (2014).
50. T. Beal, E. Massiot, J. E. Arsenault, M. R. Smith, R. J. Hijmans, Global trends in dietary micronutrient supplies and estimated prevalence of inadequate intakes. *PLoS One* **12**, e0175554 (2017).
51. C. Lachat *et al.*, Dietary species richness as a measure of food biodiversity and nutritional quality of diets. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 127–132 (2018).
52. S. J. Risch, D. Andow, M. A. Altieri, Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. *Environ. Entomol.* **12**, 625–629 (1983).
53. M. A. Altieri, The significance of diversity in the maintenance of the sustainability of traditional agroecosystems. *ILEIA Newsl.* **3**, 3–7 (1987).
54. G. Conway, *The Doubly Green Revolution: Food for All in the Twenty-First Century* (Cornell University Press, 1998).
55. A. S. Lithourgidis, C. A. Dordas, C. A. Damalas, D. N. Vlachostergios, Annual intercrops: An alternative pathway for sustainable agriculture. *Aust. J. Crop Sci.* **5**, 396–410 (2011).
56. Y. Yu, T.-J. Stomph, D. Makowski, L. Zhang, W. van der Werf, A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management. *Field Crops Res.* **198**, 269–279 (2016).
57. Y. Yu, T.-J. Stomph, D. Makowski, W. van der Werf, Temporal niche differentiation increases the land equivalent ratio of annual intercrops: A meta-analysis. *Field Crops Res.* **184**, 133–144 (2015).
58. X.-M. Xu, A simulation study on managing plant diseases by systematically altering spatial positions of cultivar mixture components between seasons. *Plant Pathol.* **60**, 857–865 (2011).
59. G. Peter, A. Runge-Metzger, Monocropping, intercropping or crop rotation? An economic case study from the West African Guinea savannah with special reference to risk. *Agric. Syst.* **45**, 123–143 (1994).
60. S. Fritz *et al.*, Mapping global cropland and field size. *Glob. Chang. Biol.* **21**, 1980–1992 (2015).
61. L. Yan, D. P. Roy, Conterminous United States crop field size quantification from multi-temporal Landsat data. *Remote Sens. Environ.* **172**, 67–86 (2016).
62. P. Calviño, J. Monzon, Farming systems of Argentina: Yield constraints and risk management. *Crop Physiol. Appl. Genet. Improv. Agron.* **51**, 70 (2009).
63. USDA National Agricultural Statistics Service, Cropland Data Layer. <https://nassgeodata.gmu.edu/CropScape/>. Accessed 6 April 2018.
64. C. Boryan, Z. Yang, R. Mueller, M. Craig, Monitoring US agriculture: The US Department of Agriculture, National Agricultural Statistics Service, Cropland Data Layer Program. *Geocarto Int.* **26**, 341–358 (2011).
65. L. Jost, Entropy and diversity. *Oikos* **113**, 363–375 (2006).
66. H. Tuomisto, A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* **33**, 2–22 (2010).
67. L. Jost, Partitioning diversity into independent alpha and beta components. *Ecology* **88**, 2427–2439 (2007).
68. K. Kobayashi, M. U. Salam, Comparing simulated and measured values using mean squared deviation and its components. *Agron. J.* **92**, 345–352 (2000).
69. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria, 2019).