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Application of Contemporary Methods for the Use of International Data in National Genetic Evaluations

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ABSTRACT

Increased international trade of genetic material from dairy cattle requires genetic evaluations across countries. Methods are discussed for comparing genetic evaluations of bulls computed in different countries. A system that combines information from several countries and produces routine international evaluations of dairy bulls is described, and possible ways of utilizing such international information in national breeding programs are presented. Important issues for international genetic evaluations are the estimation of genetic parameters within and across countries and the impact of imported bull evaluations on international rankings. Both issues are discussed in this article in view of recent research findings and potential future applications. Optimally, routine systems for international evaluation of the future will consider all economically important traits and serve different and well-defined breeding goals.
(**Key words**: international evaluation, application)

Abbreviation key: EM = expectation maximization, **INTERBULL** = International Bull Evaluation Service.

INTRODUCTION

Exchange of genetic material among countries in the form of frozen semen, embryos, and live animals intensifies as global markets become more accessible and countries turn to more intense competition for exports. The opportunity to select the best breeding animals from anywhere in the world is recognized and prompts the need for fair international comparisons among different stocks of dairy cattle.

Selection decisions are mostly based on EBV of animals for economically important traits. The EBV are commonly estimated within a country based on methods that best reflect the recording philosophy, tradition, data structure, computer capacity, and market directives of that particular country. Further, EBV within a country, hereafter referred to as national evaluations, are expressed in specific bases and scales that are unique to different countries. Therefore, utilization of foreign information based on direct comparisons between domestic and foreign national evaluations is not possible. Consequently, methods that render national evaluations comparable across countries had to be developed. Because most interest has been in male selection, emphasis has been placed on comparisons of bull evaluations.

This article reviews current methods that make foreign information of breeding animals usable at the national level. The problem is discussed from the perspectives of exporters as well as importers.

METHODS FOR INTERNATIONAL COMPARISONS OF NATIONAL BULL EVALUATIONS

Conversion of Foreign National Bull Evaluations

The oldest, most widespread method of utilizing information from another country is to convert national evaluations from that country to a base and scale that are equivalent to those used in the country of interest, which can be achieved with the use of a simple regression:

$$P_B = a + b(P_A) \qquad [1]$$

where

P_A = original national evaluation of a bull in country A,

P_B = converted evaluation of the same bull in country B,

a = intercept representing the genetic base difference between A and B, and

b = slope representing the scale ratio.

Converted evaluations of country A bulls can be directly compared with national evaluations of bulls progeny tested in country B.

Computation of conversion coefficients (a and b values) depends on existence of an adequate number of bulls with national evaluations in both countries. Minimum requirements and guidelines have been proposed by **INTERBULL**, the International Bull Evaluation Service (8).

Different variations of this method have been developed that account for accuracy of national evaluation and genetic correlation of less than unity between countries and that result in unbiased conversion coefficients (6, 23). Factors affecting the calculation and accuracy of such conversions are discussed by Powell et al. (14).

The evaluation conversion method also requires that national evaluations of bulls are properly computed in both countries. Estimation of imported bull evaluations, however, is frequently problematic because of various factors, including nonrandom mating, preferential treatment of daughters, selective use in highly diverse herds, and incomplete knowledge of foreign pedigree. Animal model applications for national evaluations, combined with proper adjustments, might solve some of these problems (e.g., selective mating and heterogeneity of variance). Further, some of the remaining problems would be partially alleviated if sire-son regressions were considered instead (i.e., sires of bulls are progeny tested in one country and their sons in another). However, long intervals are associated with such practice. Alternatively, evaluations of full sibs that were progeny tested in different countries may be considered, provided that a sufficient number of such pairs exists (11, 13).

In Model [1], country A is usually the exporter, and B is the importer. Results of this method are customized to the conditions of the importing country; that is, a joint ranking consisting of national and converted bull evaluations pertain to the breeding environment in country B. Therefore, conversion coefficients (a and b values) are computed by the importer. Bull rankings in the exporting country may not be the same if the genetic correlation between these two countries is less than unity.

To summarize, the conversion method is simple, straightforward, and easy to apply and may provide results that are appropriate for use in the importing country. However, this method is based on a relatively small number of usually selected bulls, can only be applied to two country comparisons at a time, and may not be accurate for animals with extremely high merit.

Joint Analysis of National Bull Evaluations from Several Countries

According to this method, national evaluations from several countries are jointly analyzed with a linear model. Such analysis yields international BLUP for all bulls from all countries. The following model was first suggested by Schaeffer (16):

$$y = Xc + ZQg + Zs + e \qquad [2]$$

where

y = observation vector,
c = country of evaluation effect,
g = genetic group of bull effect,
s = genetic merit of bull effect,
e = residual effect, and
$X, Z,$
and Q = incidence matrices.

The EBV from this model, hereafter referred to as international evaluations, consist of solutions for the genetic group and bull effects.

Dependent variables in Model [2] are directly related to national evaluations in each country and should represent unregressed figures of mean performance of daughters corrected for all important effects in each country. Sigurdsson and Banos (18) used simulations to compare the suitability of three different figures as dependent variables in Model [2].

1. Deregressed evaluations, resulted from removing effects from the national evaluations that are subsequently considered in Model [2].
2. Daughter yield deviations as computed in various national evaluations using an animal model (19).
3. National evaluations.

Results from this study indicated that deregressed national evaluations are the most appropriate dependent variable for Model [2].

One of the advantages of joint analysis of national evaluations is that a theoretically unlimited number of countries can be considered simultaneously. Further, all available information (national evaluations) can be used instead of information pertaining only to bulls with multiple evaluations. Some information that is not considered appropriate (e.g., import semen evaluations) can be excluded. In any case, genetic relationships among bulls are used to link information from different countries.

Application of this method presupposes that national evaluations of participating countries are un-

biased. In theory, evaluation systems using an animal model, which are now available in most countries, account for many bias sources, such as selection, assortative mating, and heterogeneity of variance. In practice, however, this consideration holds true only when the statistical model of evaluation is correct, i.e., all important sources of systematic variation in a particular country are considered. Deviations from this assumption usually result in biased national and international comparisons. A special problem regarding genetic trend estimation arises from violating the underlying assumptions (4). In such a case, ranking of animals within a country is not expected to be substantially affected. International rankings, however, would be greatly affected, especially in situations of high genetic correlations among countries, which would result in inefficient selection across countries.

Inconsistencies in genetic trend estimation in different countries have been documented (2, 4). Examples of problems with genetic trend estimation for production traits include a reported underestimation of 25% in France (3) and an overestimation of 25% (21) in the US. Provided that genetic parameters had been properly estimated (accounting for genetic trend) in an international evaluation, this trend discrepancy would have resulted in considerable overestimation of the genetic difference between young bulls from the US and France. In these two countries, corrective steps have been taken to remove the problems by including age and parity effects in the models for national evaluation. At the same time, Boichard et al. (3) proposed three methods to validate genetic trend estimation within countries. These methods are discussed in further detail in the next section.

Model [2] can be easily extended to allow for genetic correlation of less than unity between countries (17), but extension requires incorporation of the genetic (co)variance matrix among countries into the mixed model equations associated with Model [2]. Allowing for genetic correlation of less than unity appears to be desirable because differences in production systems, recording policies, or national evaluation methods may turn traits that are conceptually the same (e.g., protein yield) into different traits in each country. Further, a multitrait approach to the problem readily accommodates presence of interaction of genotype and environment.

Simulation studies (18) have indicated that Model [2] performs well in evaluations across countries given the correct genetic parameters. Fair knowledge of sire variances and genetic correlations between

countries is assumed. Genetic parameter estimation is discussed more later in this article.

The feasibility of Model [2] for international comparisons for dairy production traits has been documented in several research projects involving different bull populations (1, 2, 9, 15). Projects investigating other economically important traits are underway.

International evaluations with this method can be computed by an independent laboratory (see next section). Following the multitrait approach, different international rankings of sires can be obtained for different countries. The degree of similarity between such rankings would depend on genetic correlations between countries, which would provide a comprehensive source for importers to find the best animals for their conditions and for potential exporters to see how their animals fare in different markets.

ROUTINE INTERNATIONAL EVALUATIONS

Starting in 1994, biannual (August and February) international evaluations of bulls from several countries are computed at the INTERBULL Centre (Uppsala, Sweden) using joint national evaluation analyses with Model [2].

Data Collection and Preparation

Data are national evaluations and pedigree information of bulls that were progeny tested in various countries. A minimum accuracy criterion, based on daughters in at least 10 herds, is imposed. National evaluations of imported bulls are ignored at this stage, based on research findings that indicate problems associated with such evaluations (1). Therefore, connections between data rely on simultaneous testing of bulls in various countries and genetic relationships among bulls progeny tested in various countries.

Prior to inclusion of data from a country in the international evaluation, validation checks are made on the estimation of genetic trend. Validation methods are based on research by Boichard et al. (3) and include three procedures.

1. Comparison of genetic trends estimated using only first lactations versus all lactations normally included in the national evaluation. This process applies to evaluation systems based on repeatability models for multiple lactations and investigates the impact of cow records from different age groups on the genetic trend estimation. First lactation analyses are treated as the control.

TABLE 1. Number of records (national evaluations) considered in the international evaluation of February 1995, by country and breed.

National evaluation						
Country	Date	Ayrshire	Brown Swiss	Guernsey	Holstein	Jersey
Canada	1/95	679	75	257	5892	423
Germany	12/94	...	...	...	7437	...
Denmark	1/95	...	812	...	2973	788
Finland	12/94	3217	...	...	734	...
France	12/94	...	...	...	10,180	...
Italy	1/95	...	...	...	3717	...
Netherlands	9/94	...	...	...	5757	...
Norway	6/94	2908	...	...	...	...
Sweden	1/95	4760	...	...	2003	...
US	1/95	242	366	893	19,399	1276
Records, no.		11,806	1253	1150	58,092	2487
Bulls, no.		11,776	1214	1100	57,077	2436

2. Investigation of yearly variation of daughter yield deviations within a bull. This method may detect problems with estimation of nongenetic (environmental) trends that indirectly affect the estimation of genetic trends.

3. Analysis of variation across time of national bull evaluations. Consistency of successive national evaluations of the same bulls is assessed with this method. Impact of new daughter records on national evaluations is investigated.

Data from countries that successfully pass these tests are included in the international evaluations.

Computation of International Evaluations

International evaluations are computed with Model [2]. Dependent variables are first computed within country from national evaluations using Equation [3]:

$$y = R[A^{-1}k - A^{-1}kQ(Q'A^{-1}kQ)^{-1}Q'A^{-1}k + R^{-1}]p \quad [3]$$

where

y = vector of deregressed bull evaluations in a particular country to be used as dependent variables in Model [2],

R = diagonal matrix with diagonals equal to the reciprocal of the number of daughters of a bull in a particular country,

A = numerator relationship matrix of bulls in a particular country based on sires and maternal grandsires,

Q = incidence matrix as in Model [2],

k = scalar variance ratio assumed in a particular country, and

p = vector of national bull evaluations in a particular country.

The theory behind this procedure is described by Sigurdsson and Banos (18).

Unidentified pedigrees are grouped based on country of origin and birth year of bulls as well as path of selection (2, 17). For consistency, groups are defined in the same manner in within-country deregressions as in the international evaluation. Further, groups are considered random in order to remove linear dependencies and improve consistency in group solutions across country. Schaeffer (17) discusses the implications of such an approach.

The genetic (co)variance matrix needed to solve equations from Model [2] is currently built on the assumption that genetic correlation between countries is unity. Within-country variances are based on a pooled estimate of the within-year geometric mean of national and deregressed evaluations (1).

Current Practices

In August 1994, the first set of international evaluations computed at the INTERBULL Centre considered Ayrshire and Holstein bulls from Denmark, Finland, Norway, and Sweden (separate analysis for each breed). The second international evaluation in February 1995 considered national evaluation results from a total of 10 countries (Canada, Denmark, Finland, France, Germany, Italy, the Netherlands, Norway, Sweden, and US) and five breeds (Ayrshire, Brown Swiss, Guernsey, Holstein, and Jersey). Data used for the INTERBULL evaluation in February 1995 are shown in Table 1.

Genetic evaluations computed by this system are expressed in the base and scale of each participating

TABLE 2. Comparison of international and USDA evaluations for protein yield of US Holstein bulls born since 1980.[1]

US Bulls	Bulls (no.)	Difference		Range	Correlation[2]	DIF1
		$\overline{X}$	SE			
Only US records	10,627	−0.03	0.01	−2.87–2.61	0.999	11
Records in the US and another country	325	−0.05	0.05	−13.44–10.88	0.943	131

[1]Mean, range of differences, product-moment correlation, and number of bulls for which the difference between international and USDA evaluation exceeded 1% of the phenotypic mean of the trait (DIF1).

[2]Pooled within-year average.

country. For example, following the international evaluation in February 1995, every Holstein bull, regardless of country of origin, received nine international evaluations (one for each country included in the Holstein evaluation). Consequently, for any country, foreign bulls can be directly compared with domestic bulls, and simultaneous selection decisions within and across countries can be made.

In addition to international evaluations, conversion coefficients are computed between all pairs of countries involved. Conversion coefficients are based on international expressions of evaluation for different countries, and their computation follows INTERBULL recommendations (i.e., bulls must have daughters in at least 20 herds, must have minimum evaluation reliability of 75%, and must be born in the most recent 10 yr). These coefficients reflect differences in country solutions from Model [2] (intercept) and the sire (co)variance matrix assumed (slope). Conversion coefficients would complement international evaluations and may be used in the interim between two international evaluations when a young bull receives his first national evaluation.

Possible Uses of International Evaluations in National Breeding Programs

International evaluations from this system are based on national evaluations. Therefore, a national evaluation must take place prior to the international evaluation. Usually, results of the official national evaluation are distributed to the industry in a particular country at the same time they become available for international comparisons. Thus, domestic bulls may receive two sets of EBV for the same trait within a short time: an official national evaluation and an international evaluation. In the US, for example, official national evaluations are released in mid-January and mid-July each year. Under the current scheme, international evaluations become available about a

month later, which may confuse users of genetic evaluations. Some ideas on how such international information may be utilized in a country are discussed next.

One approach would be to disregard national evaluations and use only international evaluations. This solution appears to be straightforward and sensible as long as official national evaluations are considered in the international evaluation. Listings of international evaluations include all bulls (foreign and domestic) and are expressed in units to which industries are accustomed and therefore can be readily used. Exporters can also use these listings directly to promote their genetics abroad. The major problem is the time lag between availability of national and international evaluations. Computing national evaluations, but not making them immediately public, may not be desirable. Therefore, this approach would be acceptable only when the interval between the two evaluations is minimal.

A second approach is to use national evaluations as soon as they are computed in a country and then consider international evaluations of foreign bulls when they become available. This approach is perhaps a smoother transition from national to international evaluations; the normal timetable is maintained while additional (international) information becomes available in due course. This approach would work well if national and international evaluations of domestic bulls were the same. Because computation of the latter is based on the former, no major differences should be expected. However, additional information considered in international evaluations may create some discrepancies. The following exercise was used to illustrate this point.

National evaluations for protein yield of US Holstein bulls from the USDA evaluation in January 1995 and international evaluations of the same bulls from February 1995 were compared. The set of USDA bull evaluations used here had been computed based

TABLE 3. Examples of US Holstein bulls with the greatest difference between international and USDA evaluation.

US Bull registration	International	USDA	Difference	US Daughters	Other country	Foreign daughters
				(no.)		(no.)
Only US records						
1885561	−4	−1	−3	15	...	...
1899527	−22	−25	3	33	...	...
Records in the US and another country						
2118020	3	16	−13	20	Canada	72
2078943	7	17	−10	41	France	84
2036646	15	5	10	54	Germany	99
2026914	20	9	11	12	Germany	88

on US daughter records only. Results are shown in Tables 2 and 3. In general, evaluations of bulls that were progeny tested only in the US were very similar under the two systems. Bull genetic merit estimated with the two methods differed by more than 1% of the phenotypic mean of the trait (about 3 kg of protein on the EBV scale) for only 11 of 10,627 bulls born since 1980. Differences were observed for bulls with relatively few daughters and low reliability. In some cases, differences were because of bulls with Canadian pedigrees that were placing more emphasis on Canadian data; otherwise, differences were attributed to chance. In conclusion, for bulls that were progeny tested only in the US, use of the national evaluation and later comparison with international evaluations of foreign bulls seems safe.

For bulls that were simultaneously tested in the US and another country, however, results were different. Although, on the average, USDA and international evaluations were practically the same, differences were substantial in individual cases. Differences ranged from −13 to +11 kg for PTA for protein. Bull rankings were also somewhat affected. Differences did not show any pattern for the other country where bulls had been simultaneously tested. Also, differences appeared to be independent of time. In almost all cases of considerable difference, the USDA evaluation was based on fewer daughters than the national evaluation in the other country (Table 3), and, in general, such USDA evaluations had low reliabilities. The size of differences, however, could also reflect presence of genetic correlation of less than unity between countries, thereby violating the assumption of genetic correlation of unity for this project.

A third approach to utilizing foreign information is to use national evaluations as soon as they are computed in a country and to immediately apply conversion factors from the previous international evaluation to convert recent foreign evaluations of bulls. The time lag problem between the two evaluations disap-

pears, but this process is prone to the same limitations as the previous one. Also, this method is applicable only when genetic bases have not changed between evaluations. Under such a scenario, international evaluations are computed solely to improve the subsequent national evaluation in an individual country, and participants do not get the benefit of the most recent information available internationally.

A fourth way of using results from the previous international evaluation (international or converted evaluations) is by blending them with local information during the national evaluation process. This approach is desirable when accurate national evaluations of foreign bulls are needed (7, 10, 22). Caution should be exercised, however, to avoid counting the same information twice. Therefore, a separate procedure is needed to ascertain that information from a particular country included in international evaluation is based only on local information.

Different countries may have different views on how to utilize foreign information in their national programs. Timely delivery of national evaluations to the INTERBULL Centre for international evaluation as well as distribution of international evaluations to individual countries seems to be a key factor. Synchronization of national and international evaluations is certainly desirable but requires similar national policies toward international evaluations. Possible future moves toward continuous evaluations, both nationally and internationally, accompanied with efficient electronic data exchange, would ease some of the time-related problems.

NEW DEVELOPMENTS

Genetic Parameter Estimation

Until now, estimation of sire variance within a country has been based on a rather simple procedure (1). Further, estimation of sire covariance has been

based on the assumption of genetic correlation of unity between countries. Residual variances have then been computed from sire variances using variance ratios assumed in each country. Finally, residual effects have been assumed independent of each other, both within and across countries.

Estimation of residual variances from the data requires calculation of total sums of squares of individual (cow) observations. The latter is not available, however, in the described system of international evaluation in which data are deregressed national evaluations of bulls.

The assumption that each country uses reasonable estimates of heritability reduces the problem to estimation of sire variances. Expectation-maximization (EM) REML for a single-trait animal model with phantom groups (5) can be extended to multiple traits and considered in international evaluations with Model [2]. In a simulation study, Sigurdsson and Banos (1995, unpublished) applied this concept and used sparse matrix procedures (12) to compute sire (co)variances in two-country scenarios. Results confirmed that EM REML yield correct estimates of sire variance within country and genetic correlations between countries, provided that all available data (national evaluations) are included in the analysis. Any time-related editing that was applied to this simulated data biased estimates of genetic parameters.

The key factor to proper estimation of genetic correlations between countries with EM REML appeared to be data connectedness (Sigurdsson and Banos, 1995, unpublished), which presupposes the existence of genetic links between different bull populations. Connections between data from different countries can be direct (same bulls receive national evaluations in more than one country) or indirect (genetically related bulls are progeny tested in different countries).

Current practices exclude national evaluations for bulls with imported semen from international evaluations because of earlier evidence that such evaluations may be associated with bias (1). International evaluations, then, rely on bull performance in the country of origin. Sigurdsson and Banos (1995, unpublished) found that such a policy deprives the system of valuable direct connections between data from different countries, leading to substantial underestimation of genetic correlation. In the same study, different levels of bias were artificially introduced in national evaluations of imported bulls, and their impact on genetic correlation estimated from all available data was investigated. Results indicated that improved data connections far outweighed any possible

adverse effect of including biased information, and estimates of genetic correlation were very similar to the true values. It was concluded that evaluation data on imports should not be excluded from the estimation procedure for genetic correlation.

Impact of Foreign Bull Evaluations on International Evaluations

A study considering comparison of bulls that were progeny tested in the US, France, Germany, Italy, and the Netherlands (1) indicated that the international average merit of US bulls was being overpredicted by 20 to 25% when European evaluations of imports from US were included in the analysis. For protein yield, overestimated evaluations corresponded to 5 to 8% of the phenotypic mean. These observations prompted a decision to exclude national evaluations of imported bulls from the international evaluation.

National evaluation systems in some countries have improved since that study. In the US, for example, a new model including effects of age and parity is in place, resulting in a lower genetic trend than before. Investigation of the impact of such changes on earlier findings was undertaken.

National data from the US that had been used in the international evaluation of February 1995 were considered in separate two-country evaluations with data from France, Germany, Italy, and the Netherlands. Within country pair, separate analyses included and excluded national evaluations of US bulls in the importing (European) country; further, separate analyses considered genetic correlation of unity between countries and EM REML estimates of genetic correlation. The latter were 0.95 between US and Italy and US and France, 0.92 between US and Netherlands, and 0.90 between US and Germany.

Conversion coefficients for protein yield from US to the European countries calculated from these analyses are shown in Table 4. Differences between results based on data files that included and excluded evaluations of US imports were trivial for Italy and the Netherlands and very small for Germany. When genetic correlations of less than unity were considered, differences were practically zero. In an earlier study (1), such differences were substantial and favored the US when import data were included. Current results indicate that problems observed in the earlier study might have been largely due to discrepancies between the national evaluation systems that were in effect at that time in some of these countries. Results presented here are also supported by Weigel (20). For France, however, the impact of import evaluations on conversions was still apparent

TABLE 4. Conversion coefficients for protein yield from the US to different European countries considering different genetic correlation estimates and data files including and excluding import data.

Country	Including import data	Genetic correlation	Intercept	Slope
France	Yes	1.00	8.24	0.88
	No	1.00	3.38	0.88
	Yes	0.95	5.40	0.82
	No	0.95	2.02	0.83
Germany	Yes	1.00	21.00	0.64
	No	1.00	19.59	0.64
	Yes	0.90	18.02	0.52
	No	0.90	17.25	0.52
Italy	Yes	1.00	12.58	0.82
	No	1.00	13.47	0.82
	Yes	0.95	12.80	0.78
	No	0.95	12.95	0.77
The Netherlands	Yes	1.00	23.02	0.70
	No	1.00	23.65	0.70
	Yes	0.92	22.94	0.64
	No	0.92	23.04	0.64

and comparable with that reported by Banos et al. (1). Converted evaluations (EBV) for protein yield of US bulls were about 5 kg higher when imported data were included in the analysis and genetic correlation of unity was assumed. Genetic correlation of less than unity between France and US (0.95 in this case) reduced the bias to 3.4 kg. More studies are required to identify the optimal way of using imported bull evaluations in international evaluations. Weighing this information by a specific weight is a possible solution (20).

CONCLUSIONS AND FUTURE OUTLOOK

Routine, simultaneous genetic evaluations of dairy bulls that are progeny tested in different countries are becoming available. Such international evaluations combine data on daughter performance from several sources and provide the opportunity to utilize foreign information effectively in national breeding programs.

Current procedures for international bull comparisons utilize results of national evaluations in various countries. Therefore, international evaluations are only as good as the national evaluations of the same animals. Although advances have been made in establishing certain quality control measures (validation of genetic trend estimation), further work is needed to identify additional areas for standardization, such as optimal definition of management groups and phantom parent groups and treatment of nonadditive genetic components.

Different countries may have different policies on how internationally available information is utilized.

These policies may also change with time. Growing similarities in national policies, dictated by common needs, will increase the efficiency of use of international data and information exchange.

Flexibility of linear model analysis can result in custom joint evaluations, in which standards of bull comparison reflect local breeding conditions in a particular country. This type of evaluation would enable exporters to know which markets give them a competitive advantage and would enable importers to make wise selection decisions from different sources.

Applications to date have focused on dairy production traits, which limit the amount and usefulness of international information and entail the risk of selecting few breeding animals, thereby reducing the size of the global population. Extension of methods described in this article to cover other economically important traits must be a top priority for research.

In a rapidly internationalized environment, definition of breeding goals should not be driven by existence of selection tools. The latter should rather serve well-defined breeding goals. Availability of international evaluations for all economically important traits will serve different breeding goals in different countries and help in maintaining some of the global genetic diversity.

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