

Development of a matrix model for evaluating tree architecture regularity and its phenotypic variation patterns in *Malus* spp

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Abstract

The precise quantitative evaluation of three-dimensional tree architecture remains a major challenge in plant phenotyping research. Regularity is the macroscopic manifestation of developmental homeostasis and genetic canalization shaped during long-term plant evolution. Using 206 *Malus* spp. germplasms (encompassing species, North American cultivars, and self-bred cultivars) preserved in the National Repository of Crabapple Germplasm of China as experimental materials, this study introduces a two-dimensional matrix model into the evaluation of macroscopic three-dimensional tree architecture for the first time. By setting a coefficient of variation (CV) threshold of < 0.1 for structural traits, a tree architecture regularity matrix model [X Y Z] was constructed across three dimensions: macroscopic (X), branch (Y), and local detail (Z), from which a quantified Regularity Index (RI) was calculated. The results demonstrated the following: (1) Significant differentiation in tree architecture regularity occurred among *Malus* populations of different origins; species exhibited the highest regularity level (RI = 6.74), followed by self-bred cultivars (RI = 6.05), whereas North American cultivars showed a significantly reduced regularity index with the largest variance (RI = 4.66). (2) During artificial domestication and breeding, the local detail dimension (Z) of *Malus* was more prone to variation than its macroscopic structure, indicating that the decline in regularity followed an evolutionary pattern from local details to the overall structure. (3) Pedigree analysis of parents and offspring revealed that the RI of 25 descendant cultivars failed to exceed the maximum RI value of their respective parent species. The regularity evaluation system established in this study not only provides an auxiliary reference for the systematic classification and delimitation of *Malus* germplasms based on phenotypic evolutionary patterns, but also offers an innovative quantitative methodology and theoretical support for the early precise screening and directional breeding of tree architectural traits in woody ornamental plants.

Introduction

Tree architecture refers to the geometric structure and spatial organization of plant organs in three-dimensional space, representing a balance between endogenous growth processes and exogenous environmental constraints [1, 2], which directly influences light interception efficiency, mechanical stability, and the competitiveness for survival and reproduction [3, 4]. Studying tree architecture not only facilitates a deeper understanding of the ecological adaptation mechanisms underlying light energy interception and spatial resource allocation [5], but also serves as a crucial medium for unraveling genotype-environment interactions. Additionally, it provides a phenotypic foundation for the landscape configuration evaluation of woody ornamental plants and the directional breeding of economic trees [6]. Tree architecture is not manifested at a single scale; instead, it is a multi-layered composite structure consisting of a macroscopic outline, a branch skeleton, and local details [7]. Therefore, developing a quantitative index capable of comprehensively measuring tree architecture across both macroscopic and microscopic scales remains a key focus in current plant structural research [8].

In biology, regularity generally refers to the symmetry, high consistency, and structural stability of morphological development, serving as the macroscopic manifestation of developmental homeostasis

and genetic canalization shaped during long-term evolution [9]. Genetic canalization is defined as the ability of an organism to maintain the stable development of core phenotypes despite extrinsic environmental fluctuations or intrinsic genetic mutations [10]. The degree of phenotypic variation serves as a direct criterion for measuring developmental homeostasis and canalization, and is also a core characteristic reflecting morphological regularity [11, 12]. Studies indicate that the variation in pollen exine ornamentation is an important feature of plant evolutionary trends, and the transition from regular to irregular exine ornamentation reflects an increase in genetic diversity [13]. Accurately quantifying the degree of variation in phenotypic traits is a core prerequisite for evaluating their genetic diversity [14]. As a standardized statistic for measuring data dispersion, the coefficient of variation (CV) can effectively eliminate scale effects caused by different dimensions or sample means, thereby allowing for the comparison of variation magnitudes across different traits on a unified baseline [15]. Research on *Dalechampia scandens* [16] and ornamental *Malus* spp. [17] has confirmed that, compared to vegetative organs such as leaves, the CV of floral organ characteristics is often extremely small ($CV < 10\%$), indicating that reproduction-related traits are subjected to strictly regulated genetic control during development and possess high evolutionary conservatism [18]; in other words, a low level of phenotypic variation signifies a high level of structural regularity. Currently, as a cornerstone for assessing phenotypic stability and diversity, the CV has been widely applied in research fields such as plant germplasm resource evaluation, high-throughput phenomics, and quantitative genetics [8, 19].

The two-dimensional matrix model is a mathematical analysis tool capable of efficiently integrating multidimensional data and extracting core structural features [20]. By establishing scientific evaluation thresholds, it can convert continuous trait data into discrete binary values, thereby constructing a multidimensional matrix to achieve data dimensionality reduction and multivariate integration [21]. This model has been widely applied in fields such as complex phenotype analysis [22, 23], community ecology evaluation [24], and systems engineering [25]. Furthermore, by assigning specific weights to different hierarchical levels, the binary assignments of the multidimensional matrix can be transformed into intuitive decimal values [26]. This mathematical transformation not only retains the multidimensional structural information of the original data but also greatly simplifies the statistical comparison among complex phenotypes, providing a novel interdisciplinary analytical framework for quantifying the variation patterns of plant phenotypes [27]. Currently, it has been successfully applied in studies on plant floral organ symmetry [28] and pollen exine ornamentation regularity [23]; however, its application has rarely been reported in highly complex, cross-scale macroscopic three-dimensional spatial configurations such as tree architecture. This gap greatly restricts the elucidation of the evolutionary patterns of structural morphology in woody plants, as well as the progress of directional breeding for tree architecture and the precise evaluation of germplasm resources in ornamental trees.

Crabapples (*Malus* spp.) are plants belonging to the genus *Malus* Mill in the family Rosaceae [29, 30]. With a long cultivation history, wide distribution, and abundant germplasm resources, they are important woody ornamental plants in the North Temperate Zone [29, 30]. Under the combined influence of long-term natural evolution and artificial intervention, *Malus* spp. have developed highly variable tree architectural characteristics, encompassing various forms such as upright, spreading, weeping, and

tortuous [31]. However, current phenotypic research on *Malus* resources is mostly limited to the description and classification of traits like flower shape [32], leaf shape [33], and pollen ornamentation [34], or focuses on physiological stress resistance and molecular mechanisms [35–37]. At present, very few studies have applied quantitative methods to model and analyze the three-dimensional tree architecture of *Malus*, and there is a further lack of in-depth exploration into the macro- and micro-structural variation patterns of tree architecture among species, artificial cultivar populations, and specific parent-offspring pedigrees. This greatly restricts our understanding of the evolutionary patterns of *Malus* tree architecture and hinders the landscape configuration evaluation of woody ornamental plants as well as the directional breeding process for new tree architectural cultivars.

In view of this, using 206 *Malus* germplasms (encompassing species, North American cultivars, and Chinese self-bred cultivars) preserved in the National Repository of Crabapple Germplasm of China as experimental materials, this study introduces the concept of a two-dimensional matrix model into tree architecture for the first time. The objectives are to: (1) construct a matrix model for *Malus* tree architecture regularity encompassing macroscopic, branch, and local detail dimensions based on the trait coefficient of variation (CV), and calculate the Regularity Index (RI); (2) quantitatively analyze the variation patterns and diversity differentiation of the three-dimensional tree architecture of *Malus* among populations from different origins; and (3) explore the impacts of distant hybridization and directional selection on the regularity variation of three-dimensional tree architecture by integrating the clear breeding pedigrees of classic cultivars. This study not only provides an innovative methodological system for the quantitative evaluation of complex tree morphology in plants but also lays a theoretical foundation for the precise breeding and germplasm innovation of ornamental *Malus* tree architecture in the future.

1 Materials and Methods

1.1 Overview of the experimental site

The experimental site is located at the National Repository of Crabapple Germplasm of China in Xiannv Town, Jiangdu District, Yangzhou City, Jiangsu Province, China (119°55' E, 32°42' N). The annual average precipitation is 800–1000 mm, the annual average temperature is 16.5°C, and the frost-free period is approximately 251 days. It belongs to the northern subtropical monsoon climate with four distinct seasons. The soil type is sandy loam, which is deep and fertile, with a pH of 7.2 and a groundwater level of 1.5 m. The terrain is flat with good drainage and irrigation conditions.

1.2 Experimental materials

A total of 206 *Malus* germplasms were used in this study (Table 1), including 35 species, 94 North American cultivars (those marked with an asterisk * indicate North American cultivars with documented breeding lines), and 77 self-bred cultivars, all sourced from the National Repository of Crabapple Germplasm of China. To eliminate the influence of different rootstocks on tree growth vigor and architectural phenotypes, all tested germplasms were grafted onto *Malus hupehensis* rootstocks. The

trees were of consistent age (7–10 years old), with 10 plants per germplasm, planted in the same plot at a spacing of 2 m × 3 m. Uniform field water and fertilizer management practices were applied, and no pruning interventions were conducted on the tree architecture.

Table 1
The list of *Malus* germplasms

No.	Name	No.	Name	No.	Name	No.	Name
1	<i>Malus angustifolia</i>	53	<i>M.</i> ‘Cinderella’	105	<i>M.</i> ‘Royal Gem’	157	<i>M.</i> ‘Huanxi Sha’
2	<i>M. asiatica</i>	54	<i>M.</i> ‘Coccinella’	106	<i>M.</i> ‘Royal Raindrop’	158	<i>M.</i> ‘Hudie Quan’
3	<i>M. asiatica</i> var. <i>rinki</i>	55	<i>M.</i> ‘David’	107*	<i>M.</i> ‘Royalty’	159	<i>M.</i> ‘Jiangnan An’
4	<i>M. baccata</i>	56	<i>M.</i> ‘Dolgo’	108	<i>M.</i> ‘Selkirk’	160	<i>M.</i> ‘Jiangnan Chunxiao’
5	<i>M. baccata</i> var. <i>Mandshurica</i>	57	<i>M.</i> ‘Donald Wyman’	109	<i>M.</i> ‘Sentinel’	161	<i>M.</i> ‘Jiangnan Tianyuan’
6	<i>M. coronaria</i>	58*	<i>M.</i> ‘Eleyi’	110	<i>M.</i> ‘Shelley’	162	<i>M.</i> ‘Jiangtian Yise’
7	<i>M. domestica</i>	59	<i>M.</i> ‘Everest’	111	<i>M.</i> ‘Show Girl’	163	<i>M.</i> ‘Jingang Wan’
8	<i>M. doumeri</i>	60	<i>M.</i> ‘Fairytail Gold’	112	<i>M.</i> ‘Show Time’	164	<i>M.</i> ‘Jinqiu’
9	<i>M.</i> × <i>floribunda</i>	61	<i>M.</i> ‘Firebird’	113	<i>M.</i> ‘Snowdrift’	165	<i>M.</i> ‘Jintong’
10	<i>M. fusca</i>	62	<i>M.</i> ‘Flame’	114*	<i>M.</i> ‘Sparkler’	166	<i>M.</i> ‘Jinxin Guo’
11	<i>M. halliana</i>	63*	<i>M.</i> ‘Golden Hornet’	115	<i>M.</i> ‘Spring Glory’	167	<i>M.</i> ‘Jinxiu Jiangnan’
12	<i>M. hupehensis</i>	64	<i>M.</i> ‘Golden Raindrop’	116	<i>M.</i> ‘Spring Sensation’	168	<i>M.</i> ‘Jinyue Liang’
13	<i>M. ioensis</i>	65*	<i>M.</i> ‘Gorgeous’	117*	<i>M.</i> ‘Spring Snow’	169	<i>M.</i> ‘Jiwei Jiu’
14	<i>M. kirghisorum</i>	66	<i>M.</i> ‘Guard’	118	<i>M.</i> ‘Strawberry Jelly’	170	<i>M.</i> ‘Lanting’
15	<i>M.</i> × <i>micromalus</i>	67	<i>M.</i> ‘Harvest Gold’	119	<i>M.</i> ‘Sugar Tyme’	171	<i>M.</i> ‘Lianjuan Xifeng’
16	<i>M. orientalis</i>	68*	<i>M.</i> ‘Hopa’	120	<i>M.</i> ‘Sweet Sugartyme’	172	<i>M.</i> ‘Linjiang Xian’
17	<i>M.</i> × <i>platycarpa</i>	69	<i>M.</i> ‘Hydrangea’	121	<i>M.</i> ‘Thunderchild’	173	<i>M.</i> ‘Lvpaopao’
18	<i>M. prattii</i>	70	<i>M.</i> ‘Indian Magic’	122*	<i>M.</i> ‘Vans Eseltine’	174	<i>M.</i> ‘Orange Dream’

No.	Name	No.	Name	No.	Name	No.	Name
19	<i>M. prunifolia</i>	71	<i>M.</i> 'Indian Summer'	123	<i>M.</i> 'Velvet Pillar'	175	<i>M.</i> 'Qianceng Jin'
20	<i>M. × robusta</i>	72	<i>M.</i> 'John Downie'	124	<i>M.</i> 'Weeping Madonna'	176	<i>M.</i> 'Qianfan Jingxiu'
21	<i>M. rockii</i>	73	<i>M.</i> 'Kelsey'	125	<i>M.</i> 'White Cascade'	177	<i>M.</i> 'Qingliang Yixia'
22	<i>M. sargentii</i>	74	<i>M.</i> 'King Arthur'	126	<i>M.</i> 'Winter Gold'	178	<i>M.</i> 'Qingyu An'
23	<i>M. sieversii</i>	75*	<i>M.</i> 'Klehm's Improved Bechtel'	127	<i>M.</i> 'Winter Red'	179	<i>M.</i> 'Qingzhi Manwu'

Table 1
Cont.

No.	Name	No.	Name	No.	Name	No.	Name
24	<i>M. sieversii</i> f. <i>Niedzwetzkyana</i>	76	<i>M.</i> 'Lancelot'	128	<i>M.</i> 'Yellow Jade'	180	<i>M.</i> 'Qinyuan Chun'
25	<i>M. sikkimensis</i>	77*	<i>M.</i> 'Lemoinei'	129*	<i>M.</i> × <i>zumi</i> 'Calocarpa'	181	<i>M.</i> 'Qiuhuo Yan'
26	<i>M. spectabilis</i>	78*	<i>M.</i> 'Lisa'	130	<i>M.</i> 'Ajiao'	182	<i>M.</i> 'Qiukong Que'
27	<i>M. sylvestris</i>	79*	<i>M.</i> 'Liset'	131	<i>M.</i> 'Anni'	183	<i>M.</i> 'Qiuri Siyu'
28	<i>M. toringo</i>	80	<i>M.</i> 'Lollipop'	132	<i>M.</i> 'Bawang Bieji'	184	<i>M.</i> 'Qiuyun'
29	<i>M. toringoides</i>	81	<i>M.</i> 'Louisa'	133	<i>M.</i> 'Beiguo Zhichun'	185	<i>M.</i> 'Shanhu Hua'
30	<i>M. transitoria</i>	82	<i>M.</i> 'Louisa Contort'	134	<i>M.</i> 'Caiyun Zhuiyue'	186	<i>M.</i> 'Shanli Hong'
31	<i>M. tschonoskii</i>	83*	<i>M.</i> 'Makamik'	135	<i>M.</i> 'Chahua Nv'	187	<i>M.</i> 'Tiannv Sanhua'
32	<i>M. turkmenorum</i>	84*	<i>M.</i> 'Mary Potter'	136	<i>M.</i> 'Chanjuan'	188	<i>M.</i> 'Tiaose Ban'
33	<i>M. xiaojinensis</i>	85	<i>M.</i> 'Mays Delight'	137	<i>M.</i> 'Chudong'	189	<i>M.</i> 'Tingting Yuli'
34	<i>M. xinjinensis</i>	86	<i>M.</i> 'Molten Lava'	138	<i>M.</i> 'Chuqiu'	190	<i>M.</i> 'Wanyan'
35	<i>M. yunnanensis</i>	87	<i>M.</i> 'Neville Copeman'	139	<i>M.</i> 'Dabai Kongque'	191	<i>M.</i> 'Xiangfei'
36	<i>M.</i> 'Abundance'	88	<i>M.</i> 'Painted Scroll'	140	<i>M.</i> 'Denghuo Lanshan'	192	<i>M.</i> 'Xiangya'
37	<i>M.</i> 'Adams'	89	<i>M.</i> 'Perfect Purple'	141	<i>M.</i> 'Dianjiang Chun'	193	<i>M.</i> 'Xiangye'
38*	<i>M.</i> 'Addirondack'	90	<i>M.</i> 'Pink Prince'	142	<i>M.</i> 'Dongri Lianqing'	194	<i>M.</i> 'Xiaoer Lang'
39*	<i>M.</i> 'Almey'	91	<i>M.</i> 'Pink Spires'	143	<i>M.</i> 'Duojiang'	195	<i>M.</i> 'Xiaowei'
40	<i>M.</i> 'America Salute'	92*	<i>M.</i> 'Prairie Rose'	144	<i>M.</i> 'Fenba Lei'	196	<i>M.</i> 'Xingxing Suo'

Note: 1–35: Species; 36–129: North American cultivars (* cultivars with documented breeding lines); 130–206: Self-bred cultivars.

No.	Name	No.	Name	No.	Name	No.	Name
41	M. ‘American Spirit’	93	M. ‘Prairifire’	145	M. ‘Fendai’	197	M. ‘Xintian You’
42	M. ‘Ballet’	94*	M. ‘Professor Sprenger’	146	M. ‘Fenhong Nichang’	198	M. ‘Yipin Hong’
43	M. ‘Ballet Red’	95*	M. ‘Profusion’	147	M. ‘Gaoshan Liushui’	199	M. ‘Yutang Chun’
44	M. ‘Big Red’	96*	M. ‘Purple Prince’	148	M. ‘Hongkong Que’	200	M. ‘Zihan’
45	M. ‘Black Jade’	97*	M. ‘Radiant’	149	M. ‘Honglou’	201	M. ‘Ziou’
46*	M. ‘Brandywine’	98	M. ‘Red Baron’	150	M. ‘Hongluo’	202	M. ‘Zise Meihuo’
47	M. ‘Bride’	99	M. ‘Red Jewel’	151	M. ‘Hongqi Bing’	203	M. ‘Zitang’
48	M. ‘Butterball’	100	M. ‘Red Sentinel’	152	M. ‘Hongting’	204	M. ‘Ziwei Xing’
49	M. ‘Candymint’	101	M. ‘Red Splendor’	153	M. ‘Hongwang Zi’	205	M. ‘Ziyu Zhui’
50*	M. ‘Cardinal’	102*	M. ‘Robinson’	154	M. ‘Huamu Lan’	206	M. ‘Zi Yun Xuan’
51	M. ‘Centurion’	103	M. ‘Roger’ s Selection’	155	M. ‘Huangguo Shu’		
52	M. ‘Chestnut’	104	M. ‘Royal Beauty’	156	M. ‘Huangjin Haian’		
Note: 1–35: Species; 36–129: North American cultivars (* cultivars with documented breeding lines); 130–206: Self-bred cultivars.							

1.3 Methods

1.3.1 Extraction of characteristic variables for tree architecture regularity in *Malus*

The extraction of characteristic variables for tree architecture regularity in *Malus* was based on field measurement results. The measurements were conducted from November to December in 2024 and 2025 (after leaf fall, when the trees entered the dormant period). Observations indicated that the meteorological conditions were relatively stable over the two years, and tree architecture, as a macroscopic skeletal feature, is less affected by short-term climatic fluctuations. To improve data reliability, this study treated the observational data from the two years as a single integrated dataset to uniformly calculate the coefficient of variation (CV) for each trait. Following the principles of typicality and consistency, 10 robust, pest- and disease-free plants with uniform vigor were selected for each

germplasm, and measurements were taken on clear, windless mornings. Traits in the macroscopic dimension (X) were measured directly on the 10 selected plants; for traits in the branch dimension (Y) and the local detail dimension (Z), 3 typical main branches were selected per plant (totaling 30 main branch samples). To avoid the interference of canopy competition on tree architectural traits, healthy scaffold branches located at the outer periphery of the canopy without severe physical overlap were prioritized when selecting the main branches for measurement. All measurements were performed by the same operator to minimize human error. The specific measurement indicators and methods are as follows (Fig. 1):

Macroscopic dimension (X)

This included tree height (TH), ground diameter (GD), and crown width (CW). Tree height was measured using a height meter (accuracy ± 0.1 m); ground diameter was measured at 10 cm above the ground using a forestry diameter tape (accuracy ± 0.1 cm); crown width was determined by measuring in both the east-west and north-south directions using a measuring tape and then calculating the average.

Branch dimension (Y): This included the basal gravitropic set-point angle (GSAb), middle gravitropic set-point angle (GSAm), and distal gravitropic set-point angle (GSAd) of the main branch, as well as the spreading angle (SA) of the main branch. Main branches were defined as permanent scaffold branches growing on the central trunk, and measurements were taken using a protractor with a plumb bob, setting the direction of the gravity vector as 0° , referring to the method of Digby et al. [38]. The measurement positions were defined as follows: the base was located at 10% of the branch length from the branching point on the main trunk, the middle at 50%, and the distal end at 90%. The spreading angle was the angle between the main branch and the central trunk.

Local detail dimension (Z)

On the 30 main branches selected above, 1-year-old extension shoots and 2-year-old lateral shoots in the middle and upper parts were further randomly selected for measurement, including the internode length of 1-year-old shoot (1YIL), number of nodes on 1-year-old shoot (1YSN), number of spurs on 2-year-old shoot (2YSS), basal diameter of 1-year-old shoot (1YBD), and distal diameter of 1-year-old shoot (1YDD). The internode length of the 1-year-old shoot was the length of the stem segment between two adjacent nodes (buds or leaf scars); the number of nodes on the 1-year-old shoot was the total number of nodes contained from the base to the apex of the 1-year-old shoot; the number of spurs on the 2-year-old shoot counted the number of lateral short shoots typically ≤ 5 cm in length and possessing flower buds or leaf rosette buds; the basal and distal diameters of the 1-year-old shoot were measured using an electronic vernier caliper to determine the cross-sectional diameter at 1–2 cm from the base and 1–2 cm below the apical growing point, respectively. The distribution of traits and specific measurement locations for each dimension of *Malus* tree architecture are detailed in Fig. 1.

To enhance the expression effect of tree architecture regularity, two sub-dimensions were established for each dimension ($X_1, X_2; Y_1, Y_2; Z_1, Z_2$) [28]: macroscopic dimension X_1 (tree height, ground diameter) and

X_2 (crown width); branch dimension Y_1 (basal, middle, and distal GSA of the main branch) and Y_2 (spreading angle); local detail dimension Z_1 (internode length of 1-year-old shoot, number of nodes, number of spurs on 2-year-old shoot) and Z_2 (basal and distal diameters of 1-year-old shoot). All raw data were recorded and retained for subsequent verification.

1.3.2 Construction of the matrix model for tree architecture regularity and calculation of the regularity index

The construction of the tree architecture regularity matrix model employed a combination of binary assignment and multiplication effects. Each sub-dimension was assigned a binary value based on its average coefficient of variation (CV): 1 indicated "regular" and 0 indicated "irregular". The CV, calculated as the standard deviation (SD) divided by the mean ($CV = SD / \text{Mean}$), was used to quantify the degree of trait variation. Referring to related studies on plant phenotypic consistency, this study set $CV < 0.1$ as the regularity threshold (low variation was considered regular) [39, 40]. For sub-dimensions containing multiple traits, the arithmetic mean of the CVs of individual traits represented the regularity of that sub-dimension.

The specific assignment rules were as follows: if the average CV of the traits within a sub-dimension was < 0.1 , the sub-dimension was assigned a value of 1 (regular); otherwise, it was assigned 0 (irregular). The final assignment of each dimension was determined according to the multiplication effect rule (logical "AND" operation): a dimension was assigned a value of 1 only when both of its sub-dimensions were assigned 1; otherwise, it was assigned 0. This resulted in a 1×3 tree architecture regularity matrix $[X \ Y \ Z]$, where X represents macroscopic regularity, Y represents branch regularity, and Z represents local detail regularity.

The calculation of the Regularity Index (RI) took into account the differences in importance among the three dimensions (macroscopic regularity $X >$ branch regularity $Y >$ local detail regularity Z). The positional weight effect rule was adopted to assign weighting coefficients: the weighting coefficient is $C_j = 2^{(j-1)}$, where j is the column ordinal of the matrix (from right to left: Z is $j = 1$, Y is $j = 2$, and X is $j = 3$) [20]. Therefore, the weights were $Z = 1$, $Y = 2$, and $X = 4$, respectively. The final calculation formula for the regularity index was $RI = X \times 4 + Y \times 2 + Z \times 1$. The value of this index ranges from 0 to 7, with larger values indicating a smaller degree of variation in tree architectural traits and a higher overall regularity [20]. In this study, regularity was classified into three levels: low regularity ($RI = 0-3$), moderate regularity ($RI = 4-5$), and high regularity ($RI = 6-7$). The specific rules for regularity assignment and index calculation are detailed in Table 2.

Table 2

Assignment rules for tree architecture regularity and calculation methods for regularity index (RI) in *Malus*

Dimension	Sub-dimension	Tree architectural trait	Abbreviation	Sub-dimension regularity assignment	Dimension regularity assignment	Regularity index
X	X ₁	Tree height	TH	If $(CV_{TH} + CV_{GD}) / 2 < 0.1$, then $X_1 = 1$, otherwise 0	$X = X_1 \times X_2$	$RI = X \times 4 + Y \times 2 + Z \times 1$
		Ground diameter	GD			
	X ₂	Crown width	CW	If $CV_{CW} < 0.1$, then $X_2 = 1$, otherwise 0		
Y	Y ₁	Basal GSA of main branch	GSAb	If $(CV_{GSAb} + CV_{GSAm} + CV_{GSAd}) / 3 < 0.1$, then $Y_1 = 1$, otherwise 0	$Y = Y_1 \times Y_2$	
		Middle GSA of main branch	GSAm			
		Distal GSA of main branch	GSAd			
	Y ₂	Spreading angle	SA	If $CV_{SA} < 0.1$, then $Y_2 = 1$, otherwise 0		
Z	Z ₁	Internode length of 1-year-old shoot	1YIL	If $(CV_{1YIL} + CV_{1YSN} + CV_{2YSS}) / 3 < 0.1$, then $Z_1 = 1$, otherwise 0	$Z = Z_1 \times Z_2$	
			1YSN			
			2YSS			
		No. of nodes on 1-year-old shoot				
		No. of spurs on 2-year-old shoot				

Note: CV represents the coefficient of variation ($CV = \text{standard deviation } SD / \text{mean}$); in the assignment of regularity, 1 indicates that the trait is regular, and 0 indicates irregular; RI is the regularity index, ranging from 0 to 7, where a higher value indicates a higher degree of overall tree architecture regularity.

Dimension	Sub-dimension	Tree architectural trait	Abbreviation	Sub-dimension regularity assignment	Dimension regularity assignment	Regularity index
	Z_2	Basal diameter of 1-year-old shoot	1YBD 1YDD	If $(CV_{1YBD} + CV_{1YDD}) / 2 < 0.1$, then $Z_2 = 1$, otherwise 0		
		Distal diameter of 1-year-old shoot				
Note: CV represents the coefficient of variation (CV = standard deviation SD / mean); in the assignment of regularity, 1 indicates that the trait is regular, and 0 indicates irregular; RI is the regularity index, ranging from 0 to 7, where a higher value indicates a higher degree of overall tree architecture regularity.						

Taking the *Malus* ‘Beiguo Zhichun’ cultivar as an example (Fig. 2), based on the assignment rules for tree architecture regularity in the sub-dimensions (Table 2), the assignment results for the six sub-dimensions of *M.* ‘Beiguo Zhichun’ were: $X_1 = 1$, $X_2 = 1$, $Y_1 = 1$, $Y_2 = 1$, $Z_1 = 0$, and $Z_2 = 1$, respectively. According to the multiplication effect rule, the results calculated for the three dimensions were $X = 1$, $Y = 1$, and $Z = 0$, respectively. According to the algorithmic rule for converting binary values to decimal values, the regularity index of *M.* ‘Beiguo Zhichun’ is $RI = X \times 4 + Y \times 2 + Z \times 1 = 6$, classifying it as a germplasm with high tree architecture regularity.

1.3.3 Data processing

All data processing, statistical analyses, and graphical visualizations were performed in the R environment (version 4.3.1) [41]. The calculation of the coefficient of variation (CV) was implemented using the `sd()` and `mean()` functions; the assignment of sub-dimension regularity, construction of the tree architecture regularity matrix, and calculation of the regularity index (RI) were accomplished through custom functions. For the comparison of means in the assignment results of the X, Y, and Z dimensions and the RI among germplasms from different origins (species, North American cultivars, and self-bred cultivars), a one-way analysis of variance (ANOVA) was employed. Homogeneity of variance was tested using Levene's test, and post hoc multiple comparisons were conducted using Tukey's HSD test ($\alpha = 0.05$). Significant differences between groups were indicated by different lowercase letters ($p < 0.05$). The variation patterns of regularity among germplasms from different origins and between parents and offspring were visualized using bar charts, scatter plots, lollipop charts, and rose diagrams, and the proportion of germplasms exhibiting regularity in the X, Y, and Z dimensions was calculated for each group. All graphics were plotted using the `ggplot2` [42] package, while data manipulation and graphic layout were performed using the `dplyr` [43], `tidyr` [44], and `patchwork` [45] packages. Raw measurement data and processing scripts were saved to ensure the reproducibility of the results.

2 Results

2.1 Diversity analysis of tree architecture regularity in *Malus*

As shown by the analysis of variance for tree architecture regularity among *Malus* germplasms from different origins (Table 3), the regularity index (RI) of *Malus* populations exhibited significant statistical differences. Regarding the overall regularity (RI), the mean values of species (6.74 ± 0.66) and self-bred cultivars (6.05 ± 1.30) were relatively high, reaching the high regularity level. There was no significant difference between these two groups, but both were significantly higher than that of North American cultivars (4.66 ± 2.10 , $p < 0.05$), which fell into the moderate regularity level. This indicates that the self-bred cultivar population still maintained a high degree of regularity in its overall tree architecture, whereas the tree architecture regularity of the North American cultivar population was significantly reduced, exhibiting the largest intra-group variation (with a coefficient of variation reaching 0.45).

Regarding the assignment differences among the three dimensions—macroscopic (X), branch (Y), and local detail (Z)—both species and self-bred cultivars scored significantly higher than North American cultivars in the macroscopic (X) and branch (Y) dimensions ($p < 0.05$). However, in the local detail (Z) dimension, species (0.86 ± 0.36) exhibited higher regularity, which was significantly greater than that of the two cultivated populations (self-bred and North American cultivars, both scoring 0.57 ± 0.50). This result indicates that during the process of artificial domestication and breeding, the local detail traits of *Malus* (such as internode length, number of spurs, and shoot diameter) are more prone to variation than the macroscopic structure.

Table 3

Analysis of variance on sub-dimension assignments and regularity index (RI) of tree architecture among *Malus* germplasms from different origins

Origin	X	Y	Z	RI
Species	1.00 ± 0.00 a	0.94 ± 0.24 a	0.86 ± 0.36 a	6.74 ± 0.66 a
Self-bred Cultivars	0.96 ± 0.20 a	0.82 ± 0.39 a	0.57 ± 0.50 b	6.05 ± 1.30 a
North American Cultivars	0.73 ± 0.44 b	0.57 ± 0.50 b	0.57 ± 0.50 b	4.66 ± 2.10 b
Note: Data in the table are presented as "mean ± standard deviation". Different lowercase letters within the same column indicate significant differences at the $p < 0.05$ level according to Tukey's HSD test.				

2.2 Variation patterns of tree architecture regularity among *Malus* germplasms from different origins

To explore the distribution characteristics of regularity within populations from different origins, this study performed exponential regression fitting and visualization on the proportion of germplasms at each RI level (Fig. 3). It should be noted that because the RI is discrete data, the continuous exponential

regression equations introduced here (Fig. 3a) are solely used to intuitively and concretely visualize the regularity trends of each population, rather than serving as quantitative prediction models for discrete counts. Overall, germplasms with high regularity (RI = 6–7) were dominant, but significant differences existed in the distributions among populations of different origins. The proportion curve for the species population was the steepest ($y = 0.0002e^{1.15x}$, $R^2 = 0.87$) (Fig. 3a), primarily concentrated at RI = 7, with high-regularity germplasms accounting for 94.3% of the total (Fig. 3c). The self-bred cultivar population exhibited a similar exponential growth trend ($y = 0.0070e^{0.56x}$, $R^2 = 0.86$) (Fig. 3a), with most individuals distributed in the RI range of 5–7, and high-regularity germplasms accounting for 80.5% (Fig. 3c). In contrast, the fitted curve for the North American cultivar population was the flattest ($y = 0.0441e^{0.25x}$, $R^2 = 0.87$) (Fig. 3a), with individuals distributed across all RI levels from 0 to 7, exhibiting the most drastic variation, and high-regularity germplasms accounting for 42.6% (Fig. 3c).

Regarding the proportion of germplasms exhibiting regularity (assigned a value of 1) in each dimension (Fig. 3b), the regularity proportions of the species population in the X, Y, and Z dimensions reached as high as 100%, 94%, and 86%, respectively, demonstrating a highly regular natural tree structure. The self-bred cultivars maintained high regularity in the macroscopic and branch dimensions, at 96% and 82%, respectively. By comparison, the North American cultivars had the lowest regularity across all three dimensions (X = 73%, Y = 57%, Z = 57%), with a large number of these cultivars clustering in the moderate-to-low regularity range (RI ≤ 5) (Fig. 3c). This may be related to the hybridization and breeding history of North American crabapples, where traits such as flower color, fruit color, and disease resistance have long been the primary breeding objectives; this strong selection pressure has, to some extent, disrupted the genetic coordination of tree morphological development, leading to a reduction in tree architecture regularity.

2.3 Variation patterns of tree architecture regularity between parent and offspring *Malus* germplasms

To explore the impact of breeding pedigrees on tree architecture regularity, this study further conducted a comparative analysis between selected parent germplasms (11) and offspring cultivars (25) with well-documented pedigree records (Fig. 4, Table 4). The data revealed a distinct differentiation in tree architecture regularity between the parent germplasms and the offspring cultivars.

The distribution trend (Fig. 4a) showed that the *Malus* species used as hybridization parents had their RI highly concentrated at the maximum value of 7, with high-regularity (RI = 6–7) germplasms accounting for 81.8% and an absence of low-regularity (RI = 0–3) germplasms. In contrast, the distribution curve of the offspring population was noticeably flattened (Fig. 4a), distributing across all RI levels from 0 to 7. The variation range expanded, and the proportion of high-regularity germplasms was only 28.0%. Dimensional comparison results (Fig. 4b) further confirmed this trend: the regularity proportions of the parent germplasms in the X, Y, and Z dimensions were all at high levels (X = 100%, Y = 82%, Z = 82%); however, the regularity proportions of the offspring population in the macroscopic (X) and branch (Y) dimensions decreased significantly (dropping to 64% and 48%, respectively).

Combining the specific breeding lines in Table 4, it is evident that the RI values of all *Malus* offspring cultivars failed to exceed, and were often far below, the maximum RI values of their parent species. For example, in complex families utilizing high-regularity germplasms as core parents (such as *M. halliana*, *M. sieversii* f. *Niedzwetzkyana*, and *M. toringo*, all with an RI of 7), the offspring (such as 'Liset' with RI = 2; 'Profusion' with RI = 1; and 'Purple Prince' with RI = 4) generally exhibited low RI values. This indicates that although multi-generational hybridization enriched ornamental traits, it likely disrupted the plant's original gravitropic response and apical dominance regulatory mechanisms, resulting in a significant reduction in the regularity of tree architecture. Furthermore, the offspring cultivar 'Vans Eseltine', derived from hybridization involving *M. × floribunda* (RI = 5) and *M. spectabilis* (RI = 4), had an RI of 0, which is the lowest value among all evaluated germplasms. This suggests that *M. × floribunda* and *M. spectabilis* might not be pure species in the strict sense, but are more likely complex lines that have undergone early natural hybridization or artificial domestication.

3 Discussion

3.1 Effectiveness of the two-dimensional matrix model in revealing the variation patterns of tree architecture regularity in *Malus*

For a long time, research on tree architecture has often focused on single macroscopic indicators (such as tree height and crown width) or qualitative descriptions [46], making it difficult to comprehensively reflect its multi-layered composite structure. As a mathematical analysis tool capable of efficiently integrating multidimensional data and extracting core structural features [20], the two-dimensional matrix model has shown immense potential in plant phenotypic research. This study introduced this model into macroscopic tree architecture evaluation for the first time. By setting a coefficient of variation (CV) threshold ($CV < 0.1$), the continuous data of the macroscopic (X), branch (Y), and local detail (Z) dimensions were converted into discrete binary values to construct a binary three-dimensional data matrix [X Y Z]. Combined with the positional weight effect rule to assign different weights to the X, Y, and Z dimensions, a decimal regularity index (RI) of tree architecture was ultimately calculated. This model not only effectively eliminates the scale effects caused by different dimensions and retains the information of the plant's multidimensional spatial structure, but more importantly, it innovatively translates the abstract degree of developmental homeostasis and genetic canalization into quantifiable and comparable numerical indicators, providing an innovative methodological framework for the quantitative evaluation of complex tree morphology in woody plants. The results revealed significant differences in the tree architecture of *Malus*: the mean RI values were in the order of species (6.74 ± 0.66) > self-bred cultivars (6.05 ± 1.30) > North American cultivars (4.66 ± 2.10). This result is consistent with the findings of Zhou et al. [28] and Zhang et al. [23] regarding the symmetry of floral organs and the regularity of pollen surface ornamentation in *Malus*. Furthermore, unlike previous two-dimensional matrix models constructed based on binary qualitative traits (qualitative classification), this study innovatively adopted the precisely quantified coefficient of variation as the criterion for the binary assignment of the matrix. This transformation strategy based on continuous quantitative traits not only minimizes the subjective bias caused by manual observation to the greatest extent, but also makes the evaluation

system more rigorous and objective in a statistical sense, significantly improving the repeatability and robustness of the model in cross-spatiotemporal, large-scale phenomics measurements [22, 47].

To verify the statistical robustness of the binary assignment threshold in this evaluation model, this study conducted a sensitivity analysis of the coefficient of variation (CV) threshold. When the threshold was relaxed to $CV < 0.15$, the mean RI values of all populations became highly concentrated in the 6.8–7.0 range, losing statistical differentiation among groups (Table S1, Figure S1); whereas when the threshold was tightened to $CV < 0.05$, although the absolute RI values of all populations decreased overall and the regularity proportion in the local detail dimension (Z) approached 0 (reflecting the inherent environmental response sensitivity of microscopic traits), the RI of species and self-bred cultivars remained close and were significantly higher than that of North American cultivars ($p < 0.05$) (Table S2, Figure S2). This result not only confirms that core conclusions such as "the regularity of species is higher than that of artificial cultivars" and "the decline in regularity evolves from local to overall" possess good anti-interference capability and robustness, but also inversely corroborates that adopting $CV < 0.1$ as the baseline threshold to determine the trans-scale phenotypic developmental homeostasis of *Malus* can maximally balance the capture of biological patterns and statistical resolution. In addition, the progressive weight relationship assigned by this model (macroscopic X = 4 > branch Y = 2 > local detail Z = 1) objectively maps the synergistic evolutionary patterns of structure-function in woody plants. The study on the multidimensional functional traits of *Malus* tree architecture by Fan et al. [48] confirmed that macroscopic structure and branch biomechanical traits are the core drivers of *Malus* tree architectural differentiation, directly determining the vertical light competition and mechanical stability of the plant, and thus occupying a dominant weight in genetic canalization. In contrast, local details such as leaves are used to optimize light interception and spatial extension in microenvironments, requiring a higher degree of phenotypic plasticity; therefore, they hold a lower weight in maintaining overall developmental homeostasis. Thus, the mathematical weighting in this study quantifies the evolutionary priority of trans-scale resource allocation in plants from an ecological perspective.

3.2 The essence of variation patterns in tree architecture regularity among *Malus* germplasms from different origins

The results of this study indicate that significant differentiation exists in tree architecture regularity among *Malus* germplasms from different origins. The *Malus* species exhibited extremely high regularity, with their RI highly concentrated at the maximum value of 7, demonstrating a high degree of morphological consistency across all dimensions (Fig. 3). From an ecological perspective, three-dimensional tree architecture is the crucial foundation for plants to adapt to light interception efficiency, maintain mechanical stability, and allocate resources [49, 50]. A highly regular tree architecture enables natural species to establish stable genetic canalization mechanisms during long-term evolution, effectively buffering the interference from intrinsic genetic mutations and extrinsic environmental fluctuations, thereby maintaining the conservatism and developmental homeostasis of macroscopic phenotypes [11].

However, the tree architecture regularity of the North American cultivar population underwent extensive and drastic variation, with a large number of individuals clustered in the moderate-to-low regularity range (Fig. 3). This is likely because the long breeding history of North American crabapples has been highly focused on directional selection goals such as flower color, fruit color, and disease resistance, accompanied by frequent intrageneric interspecific distant hybridization [29, 51]. Such strong artificial selection pressure may have, to some extent, altered the genetic coordination of plant spatial development, causing a shift in the regulatory patterns of gravitropism and apical dominance [52, 53], which resulted in the lowest mean RI and the largest variance (4.66 ± 2.10) in the North American cultivar population. Due to the loss of the original buffering capacity for developmental homeostasis, a "decanalization" effect occurred, amplifying the morphological variation in microstructures [54]. This is reflected in an increased coefficient of variation for traits, especially in the local detail dimension.

In contrast, traditional Chinese garden aesthetics highly value the "tree posture" and "skeleton" of plants [55]. Over the past 20 years, the National Repository of Crabapple Germplasm of China has obtained authorization from the National Forestry and Grassland Administration of China for more than 100 new self-bred *Malus* cultivars [56]. During the breeding process, self-bred cultivars likely balanced the stability and regularity of the tree configuration to some extent while enhancing ornamental value, as seen in recent new *Malus* cultivars such as 'Chahua Nv' [57] (RI = 6) and 'Lianjuan Xifeng' [58] (RI = 6). This enabled the population to better maintain original developmental homeostasis, with their regularity index being closer to that of natural species. This indicates that current *Malus* breeding in China has achieved cultivar innovation with high tree architecture regularity while simultaneously considering ornamental traits. However, viewed dialectically from the perspective of phenotypic diversity, while the self-bred cultivar population maintains high tree architecture regularity, it also reflects a narrowing of its variation range (the population RI coefficient of variation is 0.21). Compared to the wide distribution of North American cultivars across all RI levels from 0 to 7 (with a population RI coefficient of variation up to 0.45), individuals of the self-bred cultivars are highly concentrated in the high regularity range. This phenomenon suggests that during recent breeding processes, Chinese *Malus* breeding might have tended to use a small number of natural species or core lines with excellent tree architecture as backbone parents, resulting in relatively restricted genetic backgrounds and phenotypic variation in the offspring population. Consequently, it failed to release spanning phenotypic diversity through frequent distant hybridization like the North American crabapples. Therefore, how to further broaden the dimensions of tree architecture variation in domestic *Malus* while maintaining the stability of the tree skeleton will be a direction requiring balance and breakthrough in future directional breeding.

Furthermore, this study found that the local detail dimension (Z) is more prone to variation during the breeding process compared to the macroscopic structure and branch dimensions: the proportion of regular performance in the Z dimension for both North American cultivars and self-bred cultivars decreased by 29% compared to the species (Fig. 3b). This implies that the microscopic details of plant shoots might be more sensitive to genetic recombination and environmental responses. This result also corroborates the findings of Zhou et al. [28] and Zhang et al. [23] in their studies on *Malus* floral organ symmetry and pollen surface ornamentation regularity, namely that the decline in regularity from species

to cultivars in *Malus* occurs in a direction from local to overall, reflecting a process from quantitative to qualitative change.

3.3 Implications of *Malus* tree architecture regularity on the delimitation of controversial species and breeding

In biology, a "species" is generally defined as a group of organisms with a certain natural distribution area and specific morphological and physiological characteristics [59]. Worldwide, there are 38 to 60 recognized species with valid names in the genus *Malus* [60]. However, in recent years, due to disagreements over the species concept and classification criteria, as well as the disappearance of natural distribution areas, the taxonomic status of some *Malus* taxa remains highly controversial [61]. For example, Ernie [62] proposed that *M. × micromalus* is a natural hybrid between *M. spectabilis* and *M. baccata*, and that *M. spectabilis* has no wild distribution. Li [63] suggested that *M. × floribunda* is a hybrid of *M. prunifolia* and *M. toringo*. Therefore, based on the variation patterns of *Malus* tree architecture regularity discovered in this study—that the tree architecture of species populations all possess a high regularity index, but germplasms with a high regularity index are not necessarily species; and that the decline in regularity from species to cultivars occurs in a direction from local details to the overall structure—we conducted a specific analysis on the aforementioned controversial taxa. We found that the RI of *M. baccata*, *M. prunifolia*, and *M. toringo* are all 7 ([1 1 1]), thus these germplasms are more likely to be species; the RI of *M. × micromalus* is 6 ([1 1 0]), making its status as a natural hybrid plausible; whereas the RI of *M. × floribunda* is 5 ([1 0 1]) and that of *M. spectabilis* is 4 ([1 0 0]), indicating that the regularity of these two germplasms is at a moderate level (RI = 4–5). Recent molecular and phylogenetic studies also indicate the existence of extensive interspecific hybridization and introgression within the genus *Malus*; some ornamental taxa (such as *M. × floribunda*) have hybrid origins, while other taxa (such as *M. spectabilis*) may have also experienced complex reticulate evolutionary histories [64–66]. Furthermore, the study by Zhou et al. [28] also demonstrated that *M. spectabilis* has the lowest regularity in floral organs. In summary, from the perspective of macroscopic phenotypic developmental stability, the moderate-level regularity exhibited by *M. × floribunda* and *M. spectabilis* in this study provides independent quantitative phenotypic evidence to support recent molecular phylogenetic hypotheses regarding these controversial *Malus* taxa. The regularity evaluation system established in this study innovatively provides an auxiliary reference for the taxonomic delimitation of the genus *Malus*. This also implies that, in addition to geographical distribution differences, the regularity variation patterns of multiscale phenotypes play an equally important role in species classification. Whether it is the macroscopic tree architecture and the morphology of flowers, leaves, and fruits, or the microscopic pollen ornamentation, the evolutionary patterns of these characteristics have the potential to be incorporated into the comprehensive evaluation standard system for species-level classification in the genus *Malus*.

This study also provides important implications for future *Malus* breeding: while pursuing breakthroughs in ornamental traits such as flowers, leaves, and fruits, high attention must be paid to the coordination and stability of tree architecture. In the future, the tree architecture regularity index (RI) can be utilized as

a core indicator for early precise phenotypic screening, enabling the timely elimination of inferior individuals with loose structures and disordered branching, thereby improving the breeding efficiency of new cultivars with excellent tree architecture. By precisely breeding and promoting cultivars with high regularity, high-quality germplasm resources with upright postures, stable skeletons, and greater long-term aesthetic value can be provided for landscape architecture, thereby enhancing the plants' resistance to environmental fluctuations. Moreover, the introduction of the regularity index adds a new quantitative dimension to the germplasm resource evaluation of woody ornamental plants, providing innovative methodological support for realizing the precise evaluation of landscape configurations and enhancing the scientific and artistic nature of landscape design.

3.4 Limitations and perspectives

Although the two-dimensional matrix model constructed in this study has achieved significant results in the evaluation of *Malus* tree architecture regularity, certain limitations remain. First, the development of tree architecture is a long-term dynamic process; this study only acquired static three-dimensional tree architectural data during the mature dormant period, and has not yet revealed the dynamic spatiotemporal evolutionary patterns of regularity with increasing tree age. Furthermore, as tree age increases, local light competition and shade-avoidance responses potentially triggered by the current planting density may exert fine-tuning effects on the evaluation of tree architecture regularity, which needs to be isolated and analyzed in future long-term positioning observations. Second, the coefficient of variation threshold ($CV < 0.1$) set based on phenotypic consistency theory shows good applicability in *Malus* populations, but its universal applicability in a wider range of fruit trees or forest tree species still requires further validation with massive datasets. In addition, the exploration of macroscopic tree architecture regularity in this study echoes previous research on the symmetry of *Malus* floral organs and the regularity of pollen surface ornamentation, preliminarily revealing the variation characteristics of *Malus* across trans-scale structures; however, whether this variation pattern of regularity based on developmental homeostasis widely exists in other important vegetative and reproductive phenotypes, such as leaves and fruits, remains to be systematically compared and studied in the future.

Looking forward, with the rapid development of modern plant phenomics, this regularity evaluation model is expected to be deeply integrated with unmanned aerial vehicle (UAV) light detection and ranging (LiDAR) and three-dimensional point cloud reconstruction technologies to achieve high-throughput, non-destructive, and automated extraction of three-dimensional tree architectural features in natural populations. More importantly, future research should utilize the quantified regularity index (RI) as a core phenotypic trait, and combine it with genome-wide association studies (GWAS) and multi-omics (transcriptomics, metabolomics, etc.) approaches to deeply excavate the key genes regulating the canalization of macroscopic configurations and developmental homeostasis in woody plants, thereby elucidating the molecular genetic mechanisms of tree morphological variation and artificial domestication from the underlying gene networks.

4 Conclusion

This study innovatively introduces the two-dimensional matrix model into the research of complex three-dimensional tree architectural configurations in woody plants. Based on the coefficient of variation (CV) of continuous quantitative traits, it successfully constructs an evaluation system and Regularity Index (RI) for *Malus* tree architecture regularity that encompasses multidimensional aspects including macroscopic, branch, and local details. This model effectively overcomes the difficulty of traditional tree architecture descriptions in achieving multiscale comprehensive quantification, and realizes a precise mathematical expression of plant developmental homeostasis and genetic canalization degrees. This study reveals the variation patterns of *Malus* tree architecture regularity during the evolutionary process: (1) The *Malus* species population possesses an extremely high spatial regularity of tree architecture, reflecting a stable developmental buffering mechanism formed by natural species during long-term evolution. (2) The decline in tree architecture regularity first occurs in microscopic local details, and then gradually spreads to the branches and the macroscopic entirety, embodying the phenotypic evolutionary characteristics from quantitative to qualitative change. (3) Long-term intrageneric distant hybridization and artificial selection oriented toward single ornamental traits have altered the gravitropic response and spatial developmental balance of plant growth, leading to a widespread reduction in the tree architecture regularity of offspring. In summary, this matrix model and the multiscale phenotypic variation patterns can not only serve as an auxiliary tool for defining the taxonomic status of controversial species within the genus *Malus*, but also hold broad application prospects in the directional breeding of ornamental forest trees. By utilizing the regularity index as a core quantitative indicator for early high-throughput phenotypic screening, it can effectively guide the cultivation of new plant cultivars that possess both beautiful ornamental traits and a stable, coordinated tree skeleton.

Declarations

Authorship contributions

Conceptualization, Y.F. and W.Z.; methodology, Y.F. and J.M.; software, Y.L.; validation, Y.L. and Z.H.; formal analysis, Y.F. and J.M.; investigation, Y.F. and Y.L.; resources, W.Z.; data curation, Y.F.; writing—original draft preparation, Y.F.; writing—review and editing, Y.L. and Z.H.; supervision, W.Z.; funding acquisition, W.Z. All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contribution

Conceptualization, Y.F. and W.Z.; methodology, Y.F. and J.M.; software, Y.L.; validation, Y.L. and Z.H.; formal analysis, Y.F. and J.M.; investigation, Y.F. and Y.L.; resources, W.Z.; data curation, Y.F.; writing—original draft preparation, Y.F.; writing—review and editing, Y.L. and Z.H.; supervision, W.Z.; funding acquisition, W.Z. All authors have read and agreed to the published version of the manuscript.

Data Availability

The raw trait data and R analysis scripts used to calculate the Regularity Index (RI) in this study have been deposited in Zenodo and are publicly accessible at <https://doi.org/10.5281/zenodo.21281625>.

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Table

Table 4 is available in the supplementary files section

Figures

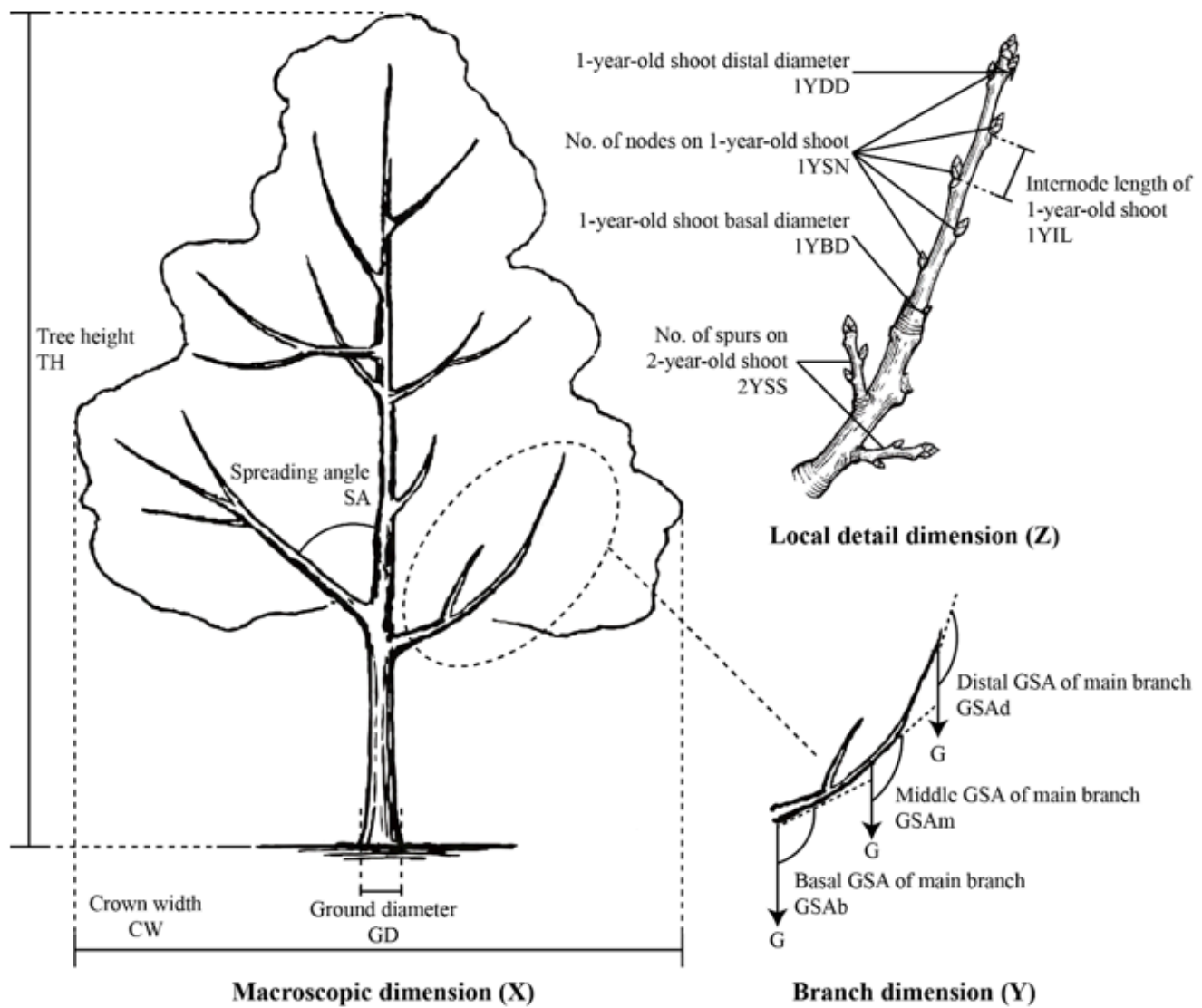
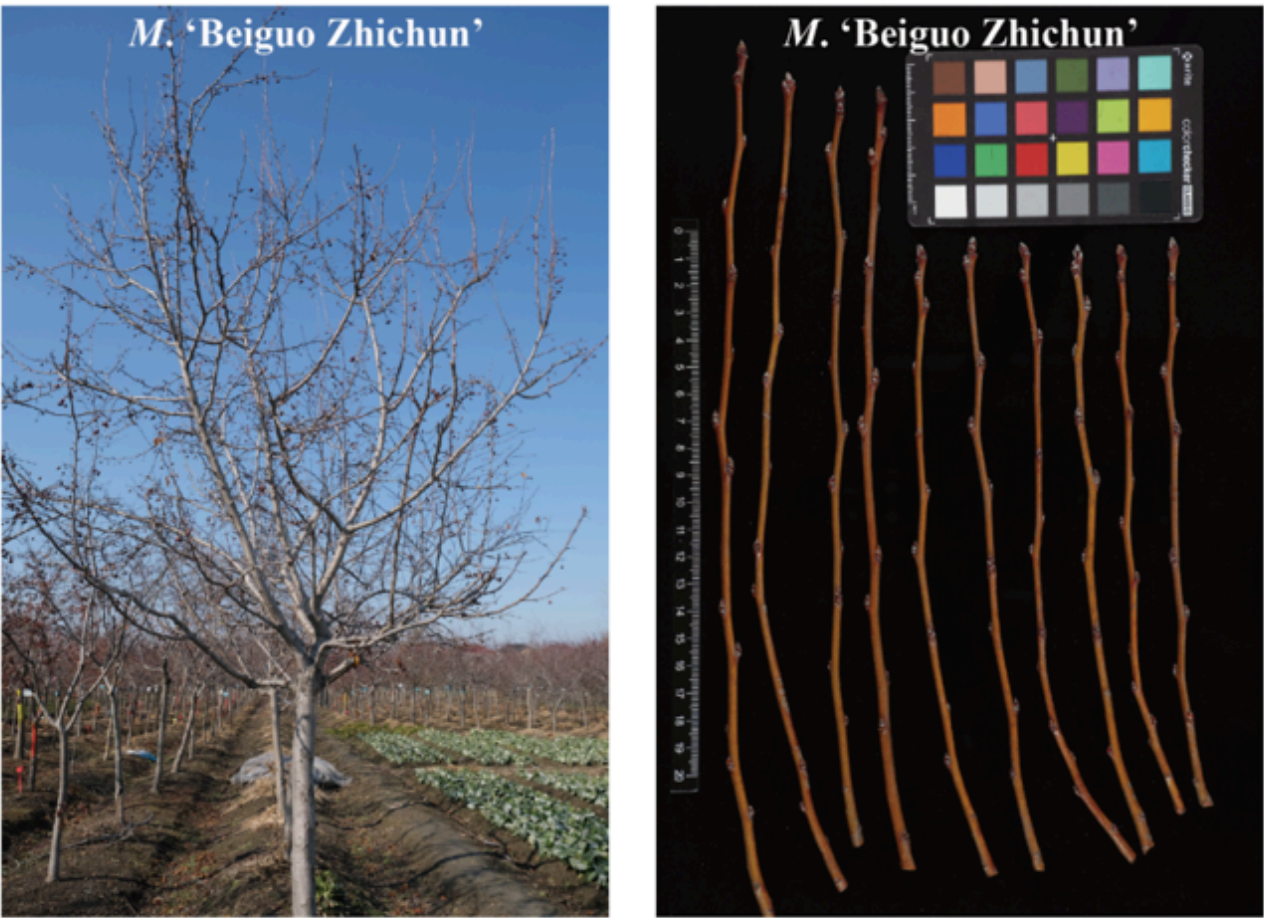


Figure 1

Schematic diagram of tree architectural traits measurement in *Malus*.



Macroscopic dimension Branch dimension Local detail dimension

Sub-dimension	X ₁	X ₂	Y ₁	Y ₂	Z ₁	Z ₂
Assignment	1	1	1	1	0	1
	}		}		}	
Dimension	X		Y		Z	
Data matrix	[1		1		0]	

Regularity index $RI = 1 \times 4 + 1 \times 2 + 0 \times 1 = 6$

Figure 2
Schematic diagram of the calculation method for RI of *M. 'Beiguo Zhichun'*.

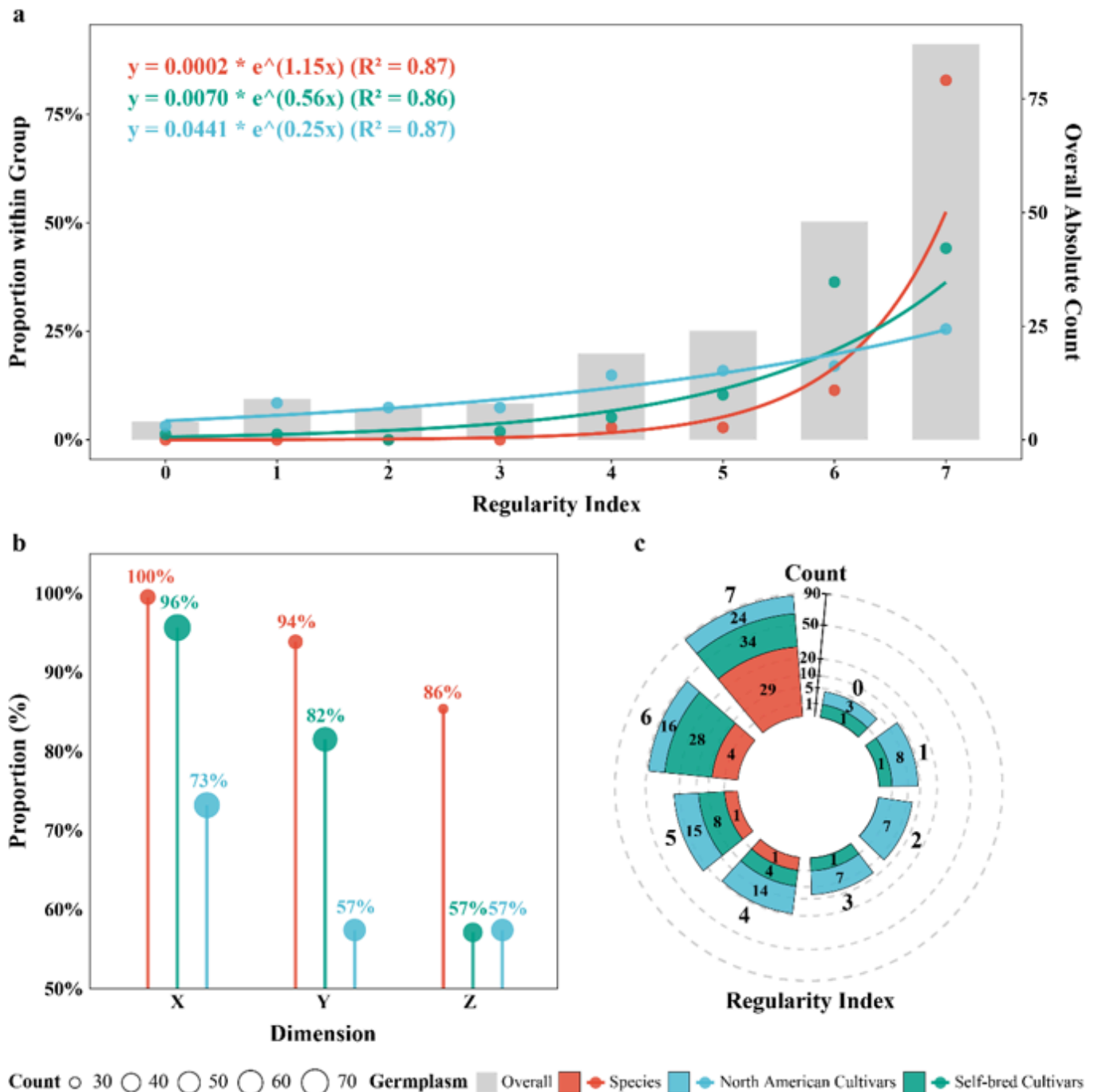


Figure 3

Distribution patterns of tree architecture regularity index (RI) among *Malus* germplasms from different origins. **a**, The intra-group proportion trends (the fitted curves are used solely to visually illustrate the distribution trends of each data group, corresponding to the left vertical axis) and overall absolute counts (grey bars, right vertical axis) of germplasms from different origins across RI levels; **b**, The proportion of germplasms exhibiting regularity (assigned a sub-dimension value of 1) in macroscopic (X), branch (Y), and local detail (Z) dimensions across different origins, where the height of the vertical lines indicates the percentage proportion within the group, and the size of the top circles represents the absolute count of

regular germplasms; **c**, The specific count distribution of germplasms from different origins at each RI level.

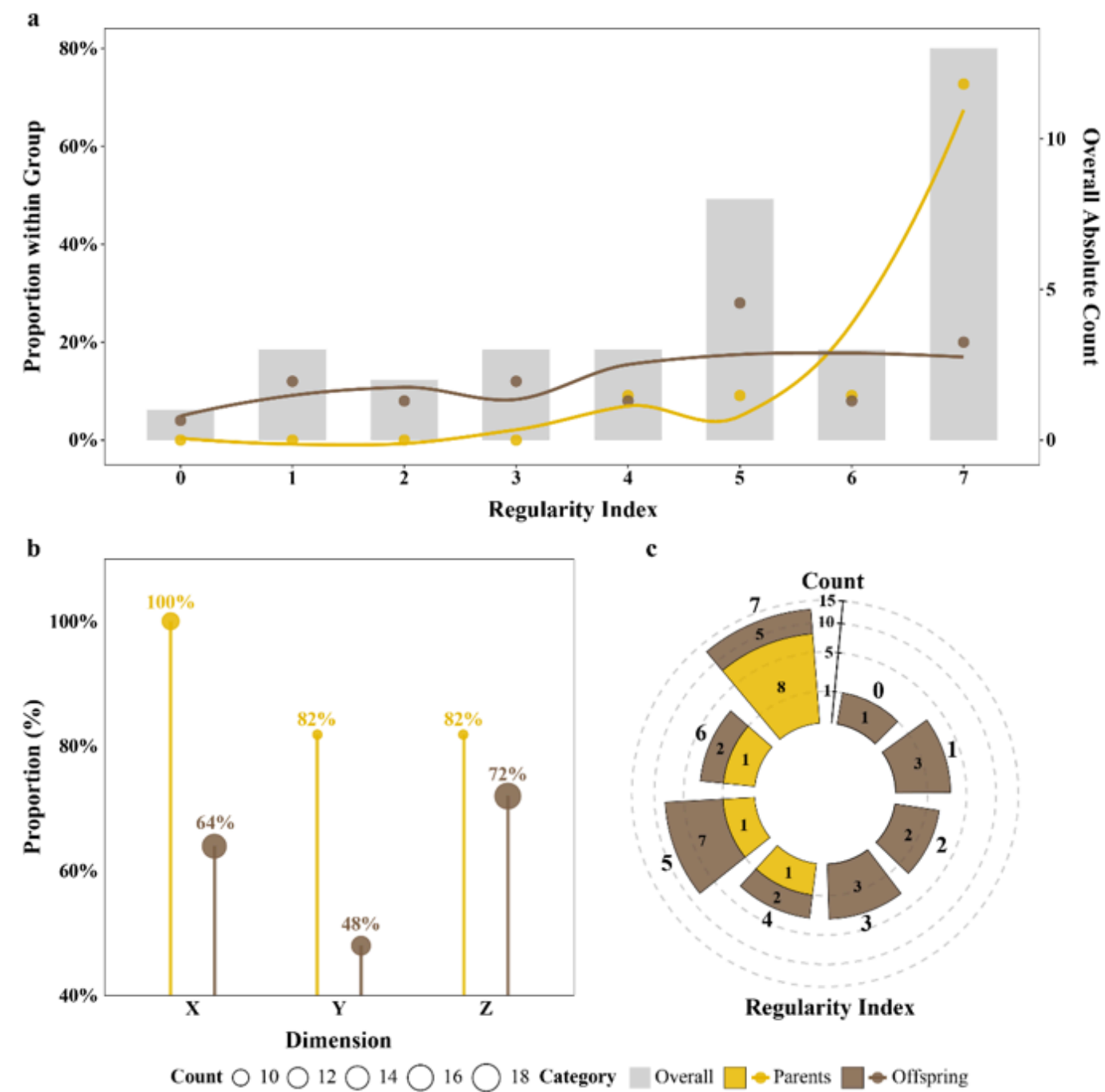


Figure 4

Distribution patterns of tree architecture regularity index (RI) between parent and offspring *Malus* germplasms. **a**, The intra-group proportion trends (the fitted curves are used solely to visually illustrate the distribution trends of each data group, corresponding to the left vertical axis) and overall absolute counts (grey bars, right vertical axis) of parent and offspring germplasms across RI levels; **b**, Comparison of the proportion of parent and offspring germplasms exhibiting regularity (assigned a sub-dimension value of 1) in macroscopic (X), branch (Y), and local detail (Z) dimensions, where the height of the vertical

lines indicates the percentage proportion within the group, and the size of the top circles represents the absolute count of regular germplasms; **c**, The specific count distribution of parent and offspring germplasms at each RI level.

Supplementary Files

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- [SupplementaryMaterials1.zip](#)
- [Table4.docx](#)