

RESEARCH ARTICLE

Acclimatization Pattern of Cultivated *Capsicum* spp. in an Agro-Ecologically Diverse Habitat, Kerala, India

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Abstract

About 135 chili accessions belonging to *Capsicum annum*, *C. chinense* and *C. frutescens* and representing various horticultural types as well as various agro-ecological zones (AEZs) of Kerala ranging from hill to coastal zone were analyzed using 18 qualitative descriptor states. Across AEZs, the distribution of species expressed variation, whereas most of the uneconomic characters did not exhibit any difference. Species-specific desirable features, secondary introduction and adaptability to environmental factors might be the possible factors behind the species-level distribution differences across AEZs. However, the absence of an association between uneconomic characters and fitness might have contributed to the lack of differences of these character states across AEZs. Selection and spread of accessions across AEZs was predominantly based on the size and weight of fruits as well as the adaptability of species. The association of climatological data with the distribution of species, horticultural types and characters worked out to elucidate possible climatic features that influenced the acclimatization. The extent of wild features retained in each species varied, which may depend on ancestor species and the intensity of selection in the domestication process. Geographical diversity analysis revealed the extent of diversity and locations of high diversity.

Keywords: Chili, Domestication, Agro-ecological zone, Secondary introduction, DIVA-GIS.

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Introduction

Chili is grown worldwide as a spice, condiment, vegetable, medicine, and ornamental plant. It belongs to the genus *Capsicum* which comprises of nearly 40 species out of which *Capsicum annum* L., *C. chinense* Jacq and *C. frutescens* L. form the major part of chili cultivation and trade around the world (Zonneveld *et al.*, 2015).

Chili is believed to have been introduced to India by Portuguese sailors. It has acclimatized well to Indian conditions, making the country the largest producer and exporter of dried chili (Anonymous, 2023). Adaptation to the diverse climatic conditions of India further proved the presence of secondary centers of diversity for cultivated species and recognition of locally adapted types. Low pungent and highly colored *C. annum* type in Jammu and Kashmir, hot chili types in the Guntur region of Andhra Pradesh, Bhut jolokia of North East India, Byadgi chili of Karnataka and Edayur chili of Kerala are examples for successful adaptations of the crop with unique characteristics supporting trade. Kerala has been identified as a secondary center of diversity for *C. chinense* and *C. frutescens* (Singh and Upadhyay, 2017).

Kerala, the state situated at the Southern end of peninsular India, has unique geographical features as a narrow strip of land between the Western ghats and the Arabian sea. Western ghats is acknowledged as one of the world's eight 'hottest hotspots of

biodiversity' (UNESCO, 2020). Based on altitude, rainfall pattern, soil type and topography, Kerala can be broadly classified into three main agro-ecological zones (AEZ): eastern hill zone, midland and western coastal plain. Western coastal plain (AEZ1) lies adjacent to the Arabian sea with an elevation of less than 30 m from mean sea level. Midland laterite zone (AEZ2) is situated between hill zone and the coastal plain with an elevation of 30 to 300 m. Eastern hill zone (AEZ3) comprises a hilly region more than 300 m above mean sea level (Rajasekharan *et al.*, 2015; KAU, 2020). Foot hills, high hills and parts of Palakkad plains with an elevation of more than 300 m are included in the Eastern hill zone (AEZ3).

Huge diversity of chili cultivars imposes a confusing task to taxonomists. To meet the needs of pepper processing industry in the United States, cultivars were classified based on fruit shape, size, texture, pungency, thickness of fruit wall, color and flavor so that similar horticultural types could be grouped together (Greenleaf, 1986; Smith *et al.*, 1987). Major horticultural types include Cayenne, Anaheim, Red chili, Serrano, Cherry, Cuban, Ancho, Waxy, Tabasco, Bell, Pimento, Squash and Jalapeno. The Cayenne group includes highly pungent chili with long, slender fruits and thin as well as wrinkled fruit surface. Anaheim chili has long fruits with medium-thick flesh and smooth fruit surfaces. They are moderate to less pungent. Red chili and Serrano are members of small hot group. As the group name indicates, it has slender fruits with high pungency. The Cherry group comprises small spherical fruits with thick flesh. Fruits of Cuban group have irregular shapes with yellowish green intermediate color. They are mildly pungent and thin-walled. Large, heart-shaped fruits with smooth surface and thin fruit walls characterize the Ancho group. The Waxy group has waxy yellow intermediate fruit color with a medium to thick fruit wall. The Tabasco group comprises slender fruits with high pungency. Other groups like Bell type, Pimento, Squash and Jalapeno have characteristic block, heart, round and cylindrical shapes, respectively.

DIVA-GIS is an updated technology that supports the exploration and analysis of gene banks and herbarium databases to elucidate genetic, ecological, and geographic patterns in the distribution of crops and wild species (Hijmans *et al.*, 2001). Not many studies have been carried out to analyze the variability of chili germplasm in Kerala based on the species level, horticultural group and agroecological zone perspectives. An attempt has been made to use the DIVA-GIS for the diversity analysis of *Capsicum* species collected from Kerala. This study evaluated the variability expressed by landraces belonging to *C. annum*, *C. chinense*, and *C. frutescens* species from three distinct agroecological zones. The inferences based on qualitative descriptors were extrapolated to analyze introduction pattern, secondary domestication features and adaptability with help of climatological data. This study is also helpful in

understanding the acclimatization pattern of an introduced crop to a rich biodiversity area.

Material and Methods

Chili accessions collected from different AEZs of Kerala *viz.*, coastal plain, laterite midland and hill zone were evaluated at Regional Station of the National Bureau of Plant Genetic Resources, Thrissur. The evaluation was carried out on 135 accessions (Table 1) belonging to three major cultivated species and representing various horticultural types. Eighteen unit characters (Table 2) per capsicum descriptor (IPGRI, 1995) representing the stages from seedling to seed were evaluated.

The latitude and longitude of collection sites were collected and mapped (Figure 1) using ArcGIS software. The distribution pattern of different species and horticultural types across the three AEZs, association of different species with unit characters and distribution pattern of different unit characters across AEZs were assessed by Chi-square analysis using SPSS 15.0. Climatological data at collection sites for a period of 30 years from 1984 was collected using NASA POWER and the relationship of various climatological features (Table 3) with the distribution of species, horticultural groups and unit characters was analyzed. DIVA-GIS version 7.5.0, free downloadable software (www.diva-gis.org), was used

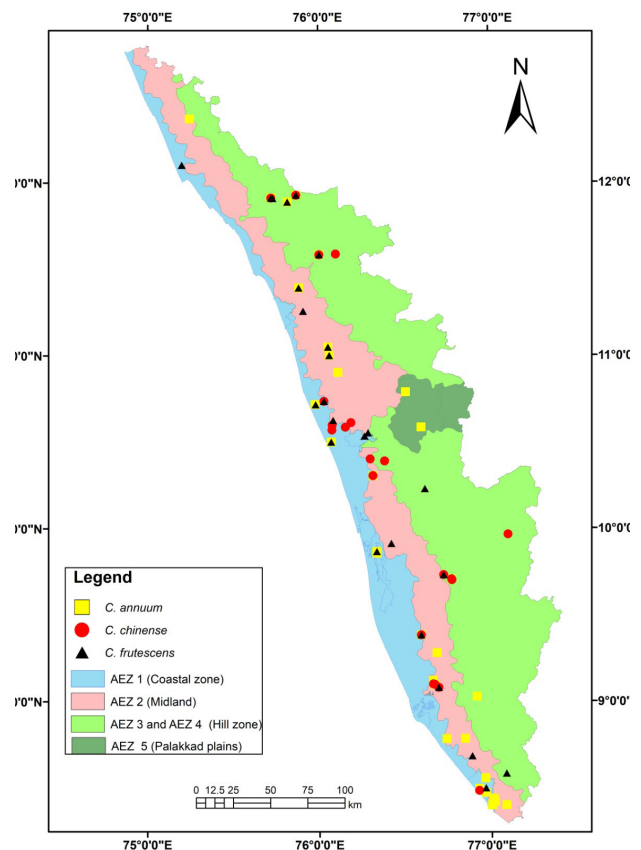


Figure 1: Geographic distribution map of chili accessions using ArcGIS

Table 1: Species, AEZ and horticultural type particulars of accessions used in the study

| Species | AEZ | Horticultural group | | | | | | | | | | | | |
|------------------------------|--------------------------|-----------------------------------|---|------------------|--------------|------------------------|--|-------------|-------------------|--|---------|---------------------------------|---------|--------------|
| | | Anaheim | Tabasco | Squash | Red chili | Cherry | Wax group | Jalapeno | Santaka | Cuban | Serrano | Ancho | Cayenne | Pimento |
| <i>C. annuum</i> (54) | AEZ-1 Coastal plane (21) | 10, 116 (2) | 9 (1) | | 22, 36G (2) | 23, 109, 36P (3) | 111, 111-I, 111-II (3) | | 35, 112, 113 (3) | 226 (1) | | 71, 110, 149, 217, 231, 235 (6) | | |
| | AEZ-2 Midland (22) | 24, 27, 28, 33, 198, 200, 242 (7) | | | 179, 180 (2) | 222 (1) | 25 (1) | 26, 161 (2) | 30 (1) | 196, 234, 236 (3) | | 162, 197, 199 (3) | | 158, 178 (2) |
| | AEZ-3 Hill zone (11) | 84 (1) | 41 (1) | | 173, 243 (2) | 86, 92 (2) | 91 (1) | | | | 46 (1) | 90, 210 (2) | | 104 (1) |
| <i>C. chinense</i> (47) | AEZ-1 Coastal plane (12) | | | 17, 144, 152 (3) | | 145, 147, 150, 244 (4) | | | 39 (1) | | | 137, 148, 153, 238 (4) | | |
| | AEZ-2 Midland (6) | | | | | | | | 190, 191, 195 (3) | | | 119, 194 (2) | | 182 (1) |
| <i>C. frutescens</i> (34) | AEZ-1 Coastal plane (10) | | 11, 13, 14, 15, 20, 21, 114, 219, 225, 260 (10) | | | 53, 85 (2) | 59, 140, 141, 142, 143, 140G, 140P (7) | | | 60, 63, 65, 66, 80, 99, 176, 245, 246, 253, 254 (11) | | 51, 54, 138, 139, 156, 177 (6) | | |
| | AEZ-2 Midland (11) | | | 61, 64 (2) | | | | | | | | | | |
| AEZ-3 Hill zone (13) | | | 43, 56, 76, 97, 101, 103, 120, 131, 187, 221, 230, 252 (12) | | | 87 (1) | | | | | | | | |

*Number of accessions assigned in each group is furnished in brackets

Table 2: Species-wise descriptor state frequencies of unit characters and Chi-square analysis of distribution of unit characters and species

| S. No. | Character | Descriptor state | Frequency | | | Chi-square value | Asymp. sig. (2-sided) |
|--------|---|------------------------|-----------------|--------------------|----------------------|------------------|-----------------------|
| | | | <i>C. annum</i> | <i>C. chinense</i> | <i>C. frutescens</i> | | |
| 1 | Shape of primary leaf | Elong-deltoid | 0.030 | 0.022 | 0.030 | 10.148 | 0.038 |
| | | Ovate | 0.200 | 0.259 | 0.178 | | |
| | | Lanceolate | 0.170 | 0.067 | 0.044 | | |
| 2 | Plant growth habit | Intermediate | 0.305 | 0.331 | 0.212 | 4.235 | 0.120 |
| | | Erect | 0.059 | 0.025 | 0.068 | | |
| 3 | Branching habit | Sparse | 0.096 | 0.037 | 0.030 | 11.443 | 0.022 |
| | | Intermediate | 0.281 | 0.296 | 0.170 | | |
| | | Dense | 0.022 | 0.015 | 0.052 | | |
| 4 | Number of flowers per axil | One | 0.326 | 0.015 | 0.052 | 69.49 | 0 |
| | | Two | 0.074 | 0.333 | 0.200 | | |
| 5 | Flower position | Pendant | 0.104 | 0.052 | 0.000 | 49.887 | 0 |
| | | Intermediate | 0.178 | 0.178 | 0.000 | | |
| | | Erect | 0.119 | 0.119 | 0.252 | | |
| 6 | Margin of calyx | Entire | 0.067 | 0.126 | 0.111 | 12.787 | 0.012 |
| | | Intermediate | 0.252 | 0.207 | 0.119 | | |
| | | Dentate | 0.081 | 0.015 | 0.022 | | |
| 7 | Stigma exertion | Inserted or same level | 0.030 | 0.089 | 0.007 | 11.346 | 0.003 |
| | | Exerted | 0.370 | 0.259 | 0.244 | | |
| 8 | Annular constriction at pedicel end | Absent | 0.363 | 0.022 | 0.244 | 99.338 | 0 |
| | | Present | 0.037 | 0.326 | 0.007 | | |
| 9 | Immature fruit position | Pendant | 0.267 | 0.170 | 0.000 | 82.023 | 0 |
| | | Intermediate | 0.015 | 0.141 | 0.015 | | |
| | | Erect | 0.119 | 0.037 | 0.237 | | |
| 10 | Mature fruit position | Pendant | 0.274 | 0.200 | 0.000 | 80.448 | 0 |
| | | Intermediate | 0.022 | 0.133 | 0.030 | | |
| | | Erect | 0.104 | 0.015 | 0.222 | | |
| 11 | Neck at the base of fruit | Absent | 0.363 | 0.215 | 0.052 | 44.08 | 0 |
| | | Present | 0.037 | 0.133 | 0.200 | | |
| 12 | Fruit shape at blossom end | Pointed | 0.333 | 0.185 | 0.244 | 23.456 | 0 |
| | | Blunt or sunken | 0.067 | 0.163 | 0.007 | | |
| 13 | Fruit blossom end appendage | Absent | 0.400 | 0.230 | 0.252 | 33.985 | 0 |
| | | Present | 0.000 | 0.119 | 0.000 | | |
| 14 | Fruit cross-sectional corrugation | Slightly corrugated | 0.363 | 0.052 | 0.207 | 73.852 | 0 |
| | | Intermediate | 0.037 | 0.185 | 0.044 | | |
| | | Corrugated | 0.000 | 0.111 | 0.000 | | |
| 15 | Fruit surface | Smooth | 0.296 | 0.007 | 0.015 | 96.395 | 0 |
| | | Semi-wrinkled | 0.089 | 0.215 | 0.237 | | |
| | | Wrinkled | 0.015 | 0.126 | 0.000 | | |
| 16 | Persistence of ripe fruit (pedicel with stem) | Slight | 0.052 | 0.244 | 0.015 | 52.791 | 0 |
| | | Intermediate | 0.274 | 0.096 | 0.193 | | |
| | | Persistent | 0.074 | 0.007 | 0.044 | | |

| | | | | | | | |
|----|--|--------------|-------|-------|-------|--------|-------|
| 17 | Persistence of ripe fruit (pedicel with fruit) | Intermediate | 0.148 | 0.156 | 0.074 | 1.978 | 0.372 |
| | | Persistent | 0.252 | 0.193 | 0.178 | | |
| 18 | Seed color | Straw | 0.385 | 0.230 | 0.230 | 19.176 | 0 |
| | | Brown | 0.015 | 0.119 | 0.022 | | |

to map diversity and analyze selected qualitative traits. The collection sites mapped with geographical coordinates were analyzed with the software in an effort to know the spatial distribution and assessment of variability for each of the aforementioned plant traits recorded. Inferences on distribution patterns and diversity were made based on the Shannon diversity index.

Characters with distinct states that could clearly distinguish wild and cultivated types such as plant growth habit, the position of pedicel at anthesis, the position of immature as well as mature fruit and the persistence of ripe fruit with pedicel, were used to construct species-wise phenograms demarcating wild and cultivated types (NTSYS 2.10z).

Results

Distribution Pattern of Various Species and Horticultural Groups Across AEZs

The distribution patterns of different species and horticultural groups are estimated, and the results are furnished in Table 1. The calculated Chi-square value for the distribution of species across AEZs was 19.435 with an asymptotic significance (2-sided) value of 0.001. *C. annuum* types were the predominant species in the coastal plane (AEZ1) and midlands (AEZ2), contributing 48.84 and 56.41% of accessions in the above two zones. A predominance of *C. chinense* was noticed in the hilly zone (AEZ3), which constituted 54.72% of accessions in that zone. Among the three cultivated species, *C. annuum* was the least represented type in the hilly zone with a representation of 20.76% only of total accessions in that zone. However, *C. frutescens* showed a more or less even distribution in the three AEZs, ranging from 38.24% in the hilly zone to 29.41% in coastal plains.

Major share of *C. annuum* accessions belonged to the Cayenne group (22.22%), followed by Anaheim (18.52%), Red chili (11.11%), and Cherry (11.11%) groups. Among *C. chinense* accessions, Cuban group was predominant (31.92%) followed by Ancho (25.53%) and Waxy groups (23.40%). Majority of *C. frutescens* accessions (97.06%) fell into the Tabasco group.

Across three AEZs, Tabasco type was the major horticultural group with 25.58, 28.21 and 24.53% representation in AEZ1, AEZ2 and AEZ3, respectively. In AEZ1, waxy type (16.28%) and Cayenne type (13.95%) were predominant after Tabasco type. Anaheim (17.95%) and Cuban (15.39%) constituted second and third positions,

respectively in distribution percentage in AEZ2. In AEZ3, Cuban (20.76%) and Waxy type (16.98%) constituted the second and third positions, respectively. The least represented groups were Pimento and Serrano types (0.74% each), which were present in AEZ3.

Distribution of Unit Characters Across Species

Distribution of unit characters and Chi-square values depicting relationships of different unit characters with cultivated species are depicted in Table 2. The distribution and relationship of each character across species are described below. Among the accessions with lanceolate shaped cotyledon, 60.53% belonged to *C. annuum*. Accessions having lanceolate cotyledon was only 19.15 and 17.65% among *C. chinense* and *C. frutescens*, respectively. A dense branching pattern was exhibited by 20.59% accessions belonging to *C. frutescens*. However, it was limited to 5.56 and 4.26% in *C. annuum* and *C. chinense*, respectively. Among the three species, accessions with sparse branching pattern were more frequent in *C. annuum* (24.07%). However, such types represented only 10.64 and 11.77% of *C. chinense* and *C. frutescens*, respectively.

Most of the *C. annuum* accessions (81.48%) were characterized by the presence of only a single flower per axil. Two or more flowers per axil were present in 95.75 and 79.41% of *C. chinense* and *C. frutescens* accessions, respectively. Among the accessions possessing two or more flowers per axil, 87.81% belonged to either *C. chinense* or *C. frutescens*. All the *C. frutescens* accessions expressed erect flower position. Among *C. annuum* and *C. chinense* species, accessions with erect pedicel were 29.63 and 34.04%, respectively. Majority of accessions belonging to *C. annuum* (44.44%) and *C. chinense* (51.06%) expressed intermediate flower position. Irrespective of species alignment, exerted stigma was prevalent in 87.41% of accessions. Among the *C. chinense* accessions, 25.53% expressed stigma at the same level of the anther lobe. This feature was limited to 7.41 and 2.94% in *C. annuum* and *C. frutescens* species, respectively. Irrespective of species type, intermediate margin was predominant in calyx. An association between *C. annuum* and dentate margin of calyx was suggested as 68.75% of accessions with dentate calyx margin belonged to the above species. Among *C. chinense* and *C. frutescens* species, it was limited to only 4.26 and 8.82%, respectively.

The presence of annular constriction could identify accessions belonging to *C. chinense*. Pseudo-annular constriction was observed among 9.26 and 2.94% of accessions belonging to *C. annuum* and *C. frutescens*,

Table 3: Chi-square analysis of climatological data with species, horticultural type and characters

| Sl. No. | Character | Earth skin temperature | | Canopy temperature | | Relative humidity | | Soil wetness | | Maximum canopy temperature | | Precipitation | | Photosynthetically active radiation (PAR) | |
|---------|-------------------------------------|------------------------|-----------------------|--------------------|-----------------------|-------------------|-----------------------|------------------|-----------------------|----------------------------|-----------------------|------------------|-----------------------|---|-----------------------|
| | | Chi square value | Asymp. Sig. (2-sided) | Chi square value | Asymp. Sig. (2-sided) | Chi square value | Asymp. Sig. (2-sided) | Chi square value | Asymp. Sig. (2-sided) | Chi square value | Asymp. Sig. (2-sided) | Chi square value | Asymp. Sig. (2-sided) | Chi square value | Asymp. Sig. (2-sided) |
| 1 | Species | 11.73 | 0.02 | 11.42 | 0.02 | 3.05 | 0.55 | 10.07 | 0.04 | 12.21 | 0.02 | 13.42 | 0.01 | 5.35 | 0.25 |
| 2 | Horticultural group | 41.42 | 0.03 | 36.22 | 0.09 | 54.48 | 0.00 | 21.14 | 0.73 | 42.34 | 0.02 | 40.78 | 0.03 | 22.02 | 0.69 |
| 3 | Shape of primary leaf | 3.34 | 0.50 | 6.24 | 0.18 | 4.84 | 0.30 | 15.84 | 0.00 | 7.57 | 0.11 | 10.78 | 0.03 | 2.97 | 0.56 |
| 4 | Plant growth habit | 2.60 | 0.63 | 1.00 | 0.91 | 13.13 | 0.01 | 2.33 | 0.68 | 3.66 | 0.46 | 7.49 | 0.11 | 0.86 | 0.93 |
| 5 | Branching habit | 5.58 | 0.23 | 7.20 | 0.13 | 0.52 | 0.97 | 15.33 | 0.00 | 3.33 | 0.50 | 3.90 | 0.42 | 3.99 | 0.41 |
| 6 | No of flowers per axil | 10.77 | 0.10 | 11.23 | 0.08 | 2.61 | 0.86 | 17.76 | 0.01 | 24.60 | 0.00 | 21.76 | 0.00 | 11.79 | 0.07 |
| 7 | Flower position | 3.07 | 0.55 | 1.13 | 0.75 | 5.58 | 0.23 | 5.60 | 0.23 | 6.42 | 0.17 | 11.70 | 0.02 | 3.03 | 0.55 |
| 8 | Margin of calyx | 5.17 | 0.08 | 5.60 | 0.66 | 1.11 | 0.57 | 0.34 | 0.85 | 0.93 | 0.63 | 0.40 | 0.98 | 4.97 | 0.08 |
| 9 | Stigma exertion | 0.07 | 0.97 | 1.76 | 0.41 | 1.00 | 0.61 | 3.38 | 0.18 | 4.21 | 0.12 | 2.72 | 0.26 | 2.07 | 0.36 |
| 10 | Annular constriction at pedicel end | 4.43 | 0.11 | 2.56 | 0.28 | 2.25 | 0.32 | 5.46 | 0.07 | 10.67 | 0.00 | 16.44 | 0.00 | 5.37 | 0.07 |
| 11 | Immature fruit position | 8.83 | 0.07 | 5.83 | 0.21 | 5.99 | 0.20 | 2.02 | 0.73 | 2.33 | 0.68 | 6.12 | 0.19 | 1.19 | 0.88 |
| 12 | Mature fruit position | 12.38 | 0.02 | 7.06 | 0.13 | 4.06 | 0.40 | 0.89 | 0.93 | 2.64 | 0.62 | 7.33 | 0.12 | 3.40 | 0.49 |
| 13 | Neck at the base of fruit | 0.73 | 0.69 | 0.93 | 0.82 | 3.90 | 0.14 | 0.78 | 0.68 | 8.12 | 0.02 | 0.02 | 0.99 | 0.62 | 0.73 |
| 14 | Fruit shape at blossom end | 9.44 | 0.01 | 7.48 | 0.00 | 1.98 | 0.37 | 3.18 | 0.20 | 4.74 | 0.09 | 0.78 | 0.68 | 2.12 | 0.35 |
| 15 | Blossom end appendage | 5.07 | 0.08 | 2.51 | 0.28 | 4.75 | 0.09 | 3.16 | 0.21 | 33.26 | 0.00 | 6.35 | 0.04 | 1.93 | 0.38 |

| | | | | | | | | | | | | | | | |
|----|--|-------|------|-------|------|------|------|------|------|-------|------|-------|------|------|------|
| 16 | Fruit cross sectional corrugation | 5.03 | 0.28 | 7.72 | 0.10 | 2.09 | 0.72 | 2.24 | 0.69 | 7.58 | 0.11 | 6.05 | 0.20 | 1.24 | 0.87 |
| 17 | Fruit surface | 16.79 | 0.00 | 13.44 | 0.01 | 1.12 | 0.89 | 7.24 | 0.12 | 22.08 | 0.00 | 11.73 | 0.02 | 5.46 | 0.24 |
| 18 | Persistence of ripe fruit (pedicel with stem) | 4.15 | 0.39 | 5.21 | 0.27 | 7.23 | 0.12 | 7.90 | 0.10 | 7.15 | 0.13 | 11.50 | 0.02 | 3.17 | 0.53 |
| 19 | Persistence of ripe fruit (pedicel with fruit) | 0.10 | 0.95 | 0.44 | 0.80 | 0.93 | 0.63 | 0.92 | 0.63 | 1.88 | 0.39 | 1.89 | 0.39 | 3.31 | 0.19 |
| 20 | Seed color | 3.04 | 0.22 | 2.46 | 0.29 | 1.29 | 0.53 | 2.25 | 0.33 | 1.59 | 0.45 | 0.94 | 0.63 | 0.78 | 0.68 |

respectively. Fruit neck was absent in majority of accessions (90.74%) coming under *C. annuum*. However, fruit neck was present in 79.41% of accessions under *C. frutescens*. Among the *C. chinense* accessions, 38.30% had fruit neck. Majority of accessions across species exhibited pointed shape at the blossom end of fruit. Among *C. chinense* accessions, 46.81% had blunt fruit end. Among *C. annuum* and *C. frutescens*, 16.67 and 2.94% of accessions had blunt fruit end. Blossom end appendage on fruit was entirely absent in *C. annuum* and *C. frutescens* accessions. However, 51.61% of *C. chinense* accessions exhibited appendages on blossom end of fruit.

About 68.52% of *C. annuum* accessions, expressed pendant fruit position at mature stage. However, 25.93% of *C. annuum* accessions had erect pedicel at mature stage. Among *C. frutescens* accessions, 88.24% were erect and the rest were semi-pendant types. Only 4.26% of *C. chinense* accessions had erect fruits. Persistence of fruit pedicel with stem was slight in most *C. chinense* accessions (70.21%); hence, the fruits were easily detachable from the plant. Easily detachable fruits were present only in 5.88 and 12.96% of *C. frutescens* and *C. annuum* accessions, respectively.

Irrespective of species alignment, most of the accessions recorded straw (yellow) seed color. The predominance of yellow seed color was evident in *C. annuum* and *C. frutescens*. Nearly 96.30 and 91.18% of accessions of the above two species exhibited this trait. The majority of the accessions (76.19%) with brown seeds, belonged to *C. chinense*. This accounted for about 34.04% of the accessions belonging to that species. Plant growth habit and ripe fruit persistence with pedicel did not express any significant variation across the species.

Distribution of Unit Characters Across AEZs

Most of the characters did not express any significant variation across different AEZs. Features that expressed significant variation across AEZs include plant growth habit, number of flowers per axil, immature fruit position, fruit shape at the blossom end, fruit blossom end appendages, and cross-sectional corrugation of fruit and fruit surface. Accessions with compact growth habit were prevalent in all the three zones. Accessions with two or more flowers per axil was predominant in AEZ1 (58.14%) and AEZ3 (75.47%).

The occurrence of accessions with blunt fruit increased progressively from AEZ1 to AEZ3 with 16.28 and 35.85%, respectively, through an intermediate 15.39% occurrence in AEZ2. Accessions from AEZ2 were characterized with the total absence of blossom fruit end appendage. In AEZ1 and AEZ3, blossom end appendage was present among 16.28 and 16.98% of accessions, respectively. AEZ1 and AEZ2, together, contributed 86.05% of accessions with smooth fruit surfaces. Among the accessions in AEZ3, 88.68% had either semi-wrinkled or wrinkled fruit surfaces. Accessions with slightly corrugated fruits amounted to 65.12 and 79.49% in AEZ1 and AEZ2, respectively whereas such types were

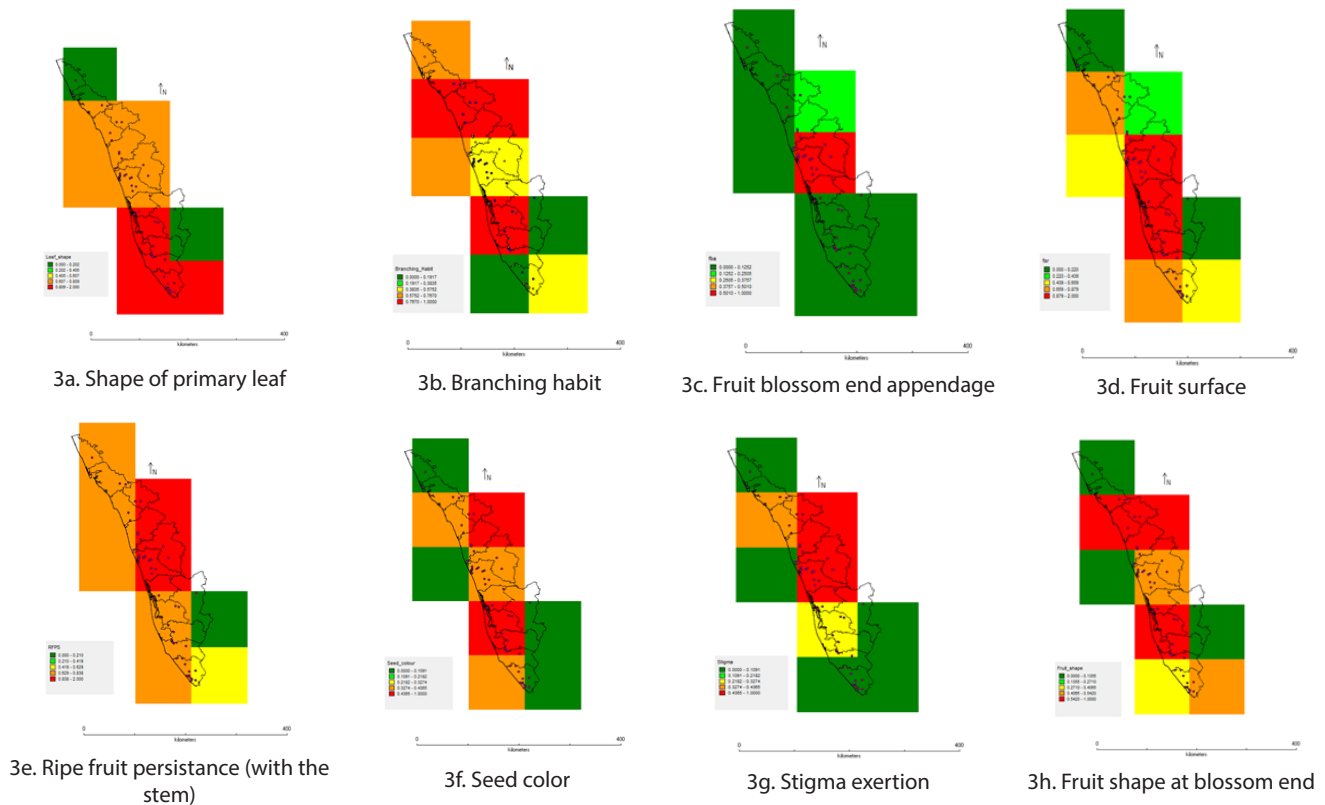


Figure 3: Diversity grid maps generated with DIVA-GIS. Grids are filled with dark green, light green, yellow, orange and red colors according to increase in Shannon diversity index

47.17% in AEZ3. AEZ3 was found to be characterized with a higher representation of accessions with intermediate to highly corrugated fruits.

Influence of Climatological Data on Species, Horticultural Type and Unit Characters

The association of climatological data with species, horticultural type and unit characters are presented in Table 3. All analyzed climatological features, except relative humidity and photosynthetically active radiation (PAR), have influenced species distribution. Among the recorded climatological features, precipitation and maximum canopy temperature had a profound role in deciding fitness of accessions with various unit characters, whereas PAR had no marked role in the same.

Species-wise Domestication Features

Species-wise dendrograms constructed based on characteristics differentiating between wild and domesticated types are presented in Figures 2a, b and c. The dendrograms demarcated wild types from domesticated in each species. Accessions that retained wild-type features accounted for 25.93 and 91.18% among *C. annuum* and *C. frutescens*, respectively. Accessions with wild features were limited to nearly 4.26% only in *C. chinense*.

Diversity Analysis using DIVA-GIS

Grid maps generated for diversity analysis of the selected traits are presented in Figures 3a to 3h. As the Shannon diversity index expresses an ascending trend, grids are filled with dark green, light green, yellow, orange and red colors.

Discussion

Acclimatization Pattern and Distribution of Species and Horticultural Types Across AEZs

A predominance of *C. annuum* was observed in the coastal zone and midlands whereas the hilly zone had higher representation of *C. chinense*. In the hilly region, *C. annuum* was the least represented species of *Capsicum*. Proportion of *C. frutescens* decreased progressively from hilly region to coastal plane. Coastal plains (AEZ1) comprise almost level to less sloping land with sandy and coastal laterite soils. Midland laterite zone (AEZ2) includes undulating lands scattered with valleys. AEZ3 comprises small hills, narrow valleys and steep slopes. The prevalence of *C. annuum* accessions in the coastal zone and midlands, as well as the increased representation of numerous horticultural types within *C. annuum*, points to the consumer and trade interests that are prevalent for that species. Similar to the

world trend, major part of the chili trade in Kerala is limited to *C. annuum* and it is the most utilized chili species (Patel *et al.*, 2011; Dhaliwal *et al.*, 2014). Marketability, early maturity, high-yielding nature and consumer preferences associated with *C. annuum* types might have led to the prevalence of that species in coastal and midland zones. Due to the steep slope, intensive and repeated agronomic operations are difficult in the hilly region. In these situations, the seasonal and annual nature of *C. annuum* makes its cultivation unattractive. Further, commercial types of *C. annuum* may not be adapted to the humid climate in hills. These factors might have contributed to widespread perennial or biennial types of *C. chinense* and *C. frutescens* in hilly zones (Smith and Heiser, 1951; Bosland and Votava, 2012). The erect and bright red colored fruits and their easy detachment from pedicel enables the birds to play a significant role in the seed dispersal of *C. frutescens* (Carvalho *et al.*, 2014). These natural seed dispersing mechanisms are well operated in less populated and ecologically undisturbed areas as in hilly zones. Further, the undisturbed ecosystem in hilly zone also confirms the maintenance of this perennial species. Extensive root system of *C. frutescens* (Singh and Upadhyay, 2017) might have also helped its adaptation to the hill slope. Increased representation of *C. frutescens* in hilly zone may be the effect of above features. Eco-geographical zone based differential distribution of species in the present study is in well agreement with origin and domestication of cultivated species of chili in South and Central America. *C. annuum* has centre of origin and centre of domestication as Mexico. *C. chinense* and *C. frutescens* originated in Amazon's river basins and domesticated at South American Plains and South-Central America, respectively. *C. baccatum* and *C. pubescens* originated in Peru-Bolivia and domesticated in low lands and high lands of Bolivia, respectively (Eshbaugh, 1970; Pickersgill, 1971; Greenleaf, 1986, Eshbaugh, 1983, Pickersgill, 1997; Bosland and Votava, 2012; Eshbaugh, 2012 and Carvalho *et al.*, 2014). Albrecht *et al.* (2012) reported significant influence of eco-geography in the genetic diversity of *C. baccatum* accessions in South America.

C. annuum accessions are grouped into 12 horticultural types. However, all except one of the *C. frutescens* belonged to the Tabasco type. The presence of different kinds of horticultural types belonging to *C. annuum* suggests the possibility of secondary introductions in that species promoted by trade and consumer interests. Bell, Pimento, Serrano and Jalapeno types belonging to *C. annuum* have only meager representation, indicating either recent introduction or hindrances in acclimatization of the above types or lack of economic advantage in farming. The occurrence of such secondary introductions are not evident in case of *C. frutescens*, represented by Tabasco type, with a prominent share across AEZs. Another reason for low variability among *C. frutescens* may be due to relatively

lower genetic variability inherent to this species than other cultivated *Capsicum* species (Carvalho *et al.*, 2015). Despite of this, *C. frutescens* exhibited variability in the present study for fruit-related features like color of immature fruits, type of fruit surface and number of fruits per axil. Present study identified six horticultural types in *C. chinense*. Bosland and Votava (2012) reported high diversity among *C. annuum* and *C. chinense* accessions and very low variability among *C. frutescens* for fruit shape. Manju and Sreelathakumary (2002) observed pronounced variability in fruit shape among *C. chinense* accessions collected from Kerala.

Prevalence of Cuban, Waxy, Cayenne, Ancho and Anaheim types points to the fact that size and weight of fruit have played a major role in deciding the selection of types for cultivation and their spread. Prevalence of pendent fruit types, irrespective of AEZs, also indicates the selection for increased fruit weight. Higher representation of *C. chinense* over *C. frutescens* in hill zone might be due to a preference for higher fruit dimensions. As the population in the three AEZs does not differ much in their consumption pattern, the adaptability of each species and horticultural type might also have a major role in deciding the cultivable area. Hence, it may be suggested that selection for yield as well as factors promoting acclimatization, might have played a prominent role in deciding the distribution of the species and horticultural types across the zones.

Species-related Unit Characters

In accordance with earlier studies, key characters and associated characters attributed to each species had expressed significant association with that species. This include lanceolate shaped cotyledon and single flower per axil in *C. annuum*; presence of annular constriction and two or more flowers per axil in *C. chinense* and one or two flowers per axil and erect flowers and fruits in *C. frutescens* (Smith and Heiser Jr. 1951; Smith and Heiser Jr. 1957; Greenleaf, 1986; Bosland and Votava, 2012 and Carvalho *et al.*, 2014). The present study indicated that majority of *C. annuum* germplasm had comparatively dentate calyx margin and *C. chinense* had easily detachable fruits from plant.

Distribution of Unit Characters Across AEZs

Most of the uneconomic characters did not exhibit any significant difference across AEZs. As the chance for artificial selection for above characters is very limited, forces that are operating to make variations among populations include mutation, migration and natural selection. These forces also seem to have failed to bring out significant differences in the phenotypic frequency of the above traits across the zones. As the fixation of alleles controlling these uneconomic characters occurred in a similar pattern in all the AEZs, it may be inferred that these characters are not associated with fitness. The minimal role of natural selection leading to the formation of distinct populations differing

in phenotypic frequency according to microclimatic environments may be due to lack of initial genetic variability as chili is an introduced crop. Pickersgill (1997) reported reduced variation in less noticeable characters in chili due to founder effects associated with domestication. Characters that expressed differentiation across AEZs were mostly secondary taxonomic characters whose association with AEZ was due to differential species distribution across AEZs.

Influence of Climatic Features on AEZ-wise Expression Pattern

We may now discuss the climatic features that influenced the AEZ-wise differential distribution of species, horticultural types and other traits. As evidenced from Table 3, canopy temperature, maximum canopy temperature, earth skin temperature, soil wetness and precipitation had role in influencing species distribution patterns. Climatological features deciding AEZ-wise distribution of horticultural groups include relative humidity, precipitation, earth skin temperature and maximum canopy temperature. Among the climatic features analyzed, only relative humidity significantly influenced growth habits with an AEZ-specific expression pattern. Rather than individual climatological features, species-specific distribution may lead to AEZ-wise differential expression of number of flowers per axil, fruit position, fruit shape at blossom end, and cross-sectional corrugation of fruit and fruit surface as these are mostly species-associated features. This was evident from Chi-square analysis as flower position, immature fruit position, and fruit cross-sectional corrugation did not express any significant association with any of the analyzed climatological features. The same pattern was expressed by the calyx margin of fruit, ripe fruit persistence with fruit, seed color and stigma exertion. The difference in morphological characters in chili according to climatic features of place of origin is in agreement with a previous report (Albrecht *et al.*, 2012).

Species-wise Domestication Features

As the weight of fruit increases, the pedicel becomes pendant to accommodate the increased weight. Human selection for increased fruit size and weight might have resulted in pendant fruits in cultivated varieties. However, the wild types have brightly colored fruits with erect pedicels which are clearly visible from above the canopy help in their dispersal by birds. Easy detachment of fruits from pedicel also aids in the dispersal (Carvalho *et al.*, 2014). Present study revealed the preference for increased size and weight of fruit across AEZs from the preponderance of accessions with pendant fruits.

Majority of accessions belonging to *C. frutescens* have expressed wild characteristics. Among the *C. frutescens* accessions, only 8.82% expressed domesticated traits and are found to be characterized with bending down of pedicel upon fruit maturity due to larger fruit size. These accessions

might have evolved due to the selection for size and weight of fruits. Carvalho *et al.* (2014) reported that *C. frutescens* is the most preserved species among the domesticated forms of *Capsicum* as the shape, size and color of fruits were conserved across wild and domesticated forms of that species.

Compared to other species, the domestication trend was intense among *C. chinense*. Among the *C. chinense* accessions, 95.75% belonged to domesticated groups with intermediate or pendant fruit pedicel. This throws light on the intense selection practiced for fruit weight in these types. Further, the fruits of most of the *C. chinense* accessions were easily detachable from the plant, making harvesting less cumbersome. The proportion of accessions with inserted stigma were also higher in *C. chinense*, resulting in higher fruit set than other species. Comparatively less exertion of style and stigma in *C. chinense* was also reported by Eshbaugh (2012). Eshbaugh (1970) and Pickersgill (1971) postulated that *C. chinense* originated from *C. frutescens* gene pool. The intense level of domestication observed may be the result of evolution from an already domesticated species and the introduction of such domesticated materials.

C. annuum accessions also exhibited a high degree of wild nature. Nearly 25.93% of *C. annuum* accessions expressed erect fruit position. The higher degree of wild nature may be due to presence of ornamental type chilies with erect fruit pedicel included in the present study. Another reason for the increased presence of wild types among *C. annuum* germplasm may be selection for bushy, early flowering and compact plant types, resulting in fasciculate flowering types and erect fruit bunch types (Elitzure *t al.*, 2009).

Diversity Analysis on a Geographical Scale

Geographical information systems has been a valuable tool in natural resources management in India *viz.*, watershed management, land use planning etc. DIVA-GIS is a geographic information system (GIS) designed to assist the plant genetic resource explorers and biodiversity communities to map the range of distribution of species they are interested in (Hijmans *et al.*, 2000). However, it is less used for plant genetic resources management in India. DIVA-GIS enable us to understand and comprehend the distribution of diversity on a geographical scale and also help in identifying gaps in germplasm collection.

Traits *viz.*, plant growth habit, flower position, neck at base of fruit, fruit cross-sectional corrugation, smoothness of fruit surface, calyx margin of fruit, mature fruit position, ripe fruit persistence with pedicel, number of flowers per axil and fruit shape at blossom end had high Shannon diversity index indicating presence of diverse accessions for the above traits throughout the state. Most of the above traits do not have primary economic importance like yield. It could be assumed that economically important traits may not be associated with above traits and so the cultivated germplasm preserves diverse accessions for such traits.

Another reason is species association of above traits and presence of multiple species in each location. For example, *C. annuum* had almost round cross-sections, whereas *C. chinense* has corrugated cross-sections. Similarly, *C. chinense* mostly had pendant or intermediate fruit position whereas *C. frutescens* had an erect fruit position. On the contrary, traits viz., fruit blossom end appendage and stigma exertion have low Shannon diversity index throughout state. This low diversity index may be due to genetic bottleneck as the introduced material has low diversity for these traits. Some traits have localized centers of diversity. For example, ripe fruit persistence with stem has diverse genotypes in Malappuram, Thrissur and Palakkad. Seed color has diverse accessions in Wayanad, Kozhikkode, Kottayam, and parts of Pathanamthitta. Similarly, Kottayam, Alleppy, Pathanamthitta and parts of Ernakulam and Kollam had diverse accessions with respect to branching habits. For fruit shape at the blossom end, diverse accessions were present in Kannur, Kozhikkode, Wayanad, Malappuram, Ernakulam, Kottayam, Alleppy and Pathanamthitta. Immature fruit position, primary leaf shape and flower position have higher diversity in Southern Kerala, whereas ripe fruit persistence with stem and branching habit had higher diversity towards Northern Kerala. This information could be used to decide exploration sites for the above traits. DIVA-GIS mapping may be effectively used for diversity analysis, identifying gaps in collection and distribution patterns and developing new conservation strategies, particularly in the wake of recent international developments related to food and nutritional security. GIS mapping has been successfully used in assessing biodiversity (Varaprasad *et al.*, 2008) and in identifying areas of high diversity in black gram (Abraham *et al.*, 2010); *Phaseolus* bean (Jones *et al.*, 1997); wild potatoes (Hijmans *et al.*, 2003); horse gram (Sunil *et al.*, 2008); *Jatropha curcas* (Sunil *et al.*, 2009); linseed (Sivaraj *et al.*, 2009; 2012); *Canavalia* (Sivaraj *et al.*, 2010); onion (Kamala *et al.*, 2011); and medicinal plants (Varaprasad *et al.*, 2007).

Conclusion

The distribution pattern of *Capsicum* species across AEZs was found to be based on superiority for economic traits and adaptability to environmental factors. Selection in favor of increased fruit size and weight was evident across AEZs. The extent of domestication was intense in *C. chinense*, whereas it was the lowest in *C. frutescens*. This reveals the role of ancestor relationships and selection pressure. The present study elucidated the AEZ-wise differential distribution of species and horticultural types. Integration of omics information with edaphic-climatic conditions prevailing in the AEZs could reveal genomic and molecular basis of acclimatization. This could be further utilized to develop AEZ-specialized cultivars with beneficial GxE interaction.

Diversity analysis on the geographical scale could be used to decide future study exploration sites.

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