

Geographic spatial autocorrelation of morphological characters of the *Hemerocallis middendorffii* complex (Liliaceae)

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A spatial autocorrelation analysis of 11 quantitative characters among 31 populations of the *Hemerocallis middendorffii* complex (Liliaceae) in Japan and Korea was conducted to better understand their patterns of geographic variation. There are two types of relationships between the mean values of the characters measured and their spatial autocorrelations: (1) significant heterogeneity of means with significant autocorrelation (length of inflorescence [LIF], length of perianth tube enclosing ovary [LPO], length of inner [LIP] and outer [LOP] perianth), and (2) significant heterogeneity of means with weak autocorrelation (width of inner and outer perianth and mostly vegetative characters). LIF displays a clear geographical (altitudinal, longitudinal, and latitudinal) cline, indicating that shorter inflorescences are generally located in northern, alpine and subalpine populations. In addition, LPO, LIP, and LOP show clear altitudinal and longitudinal variation. Floral tube and perianth length in the eastern and lowland populations are generally shorter and smaller than those in alpine, subalpine and western populations. The paleoclimatic history during the Quaternary period and diverse ecological conditions (e.g., altitudinal, longitudinal, and latitudinal differences) in the Japanese archipelago probably operated in shaping the patterns of local differentiations now recognized in the *H. middendorffii* complex.

Key words: *Hemerocallis middendorffii* complex, geographic variation, morphology, spatial autocorrelation

INTRODUCTION

Species of the *Hemerocallis middendorffii* complex (*sensu* Noguchi 1986) of the Liliaceae occur widely in East Asia, from northeastern China and

northern and central Korea, north to southeastern Siberia, and east to central Honshu and Hokkaido of Japan, and Urup Island of the Kuril Islands. The complex also grows in exceedingly diverse ecological conditions. According to Noguchi (1986),

the complex in Japan occurs in diverse habitats, ranging from sea level to an elevation of 2 400–2 500 m a.s.l. (e.g., alpine meadows) in central Honshu. The wide distribution and exceedingly diverse habitats have resulted in considerable geographical variation in morphological traits. Thus, the taxonomy of the complex has been controversial in the past 30 years (Matsuoka & Hotta 1966, Noguchi 1986). For a better understanding on the mode of differentiation of local populations in Japan, Noguchi (1986) conducted morphological analyses (e.g., principal components and cluster analyses) based on 34 localities throughout the range of the complex in Japan. She noted that the characters for reproductive organs showed a narrow range of variability, whereas the vegetative characters were highly variable. She also noted that the length of the perianth tube enclosing an ovary and the length of the internal and external perianth exhibited geoclineal (latitudinal) variation. As local differentiation within the complex has taken place in a complicated manner due to exceedingly diverse ecological conditions, it would be important to analyze critically the patterns of altitudinal variation in morphological characters in conjunction with the latitude and longitude of habitats where the complex occurs.

The principal method of analysis for this purpose is spatial autocorrelation analysis. Spatial autocorrelation statistics are a summary measure of the dependence of the value of a particular variable at one location on the value of that same variable at other nearby locations. The most commonly used measure is Moran's (1950) autocorrelation coefficient I , in which geographic neighbors are

compared in terms of their deviation from the mean of all observations. Recently, this method of character analysis has been employed in the analysis of morphological characters and the spatial dispersal patterns of genetic variation among populations because it can provide a detailed picture of geographic variation in characters (Sokal & Oden 1978a, 1978b, Jensen 1986, Sokal *et al.* 1986, Chung 1995, 1996, Kang *et al.* 1997).

A detailed study of the patterns of geographic (altitudinal, longitudinal, and latitudinal) variation of quantitative morphology is reported here for the *Hemerocallis middendorffii* complex. It is expected that the results obtained from this study may provide a better understanding as to the rate and mode of adaptive radiation in the complex as well as species groups with similar ecological and distributional patterns in East Asia.

MATERIALS AND METHODS

Measurements of 11 external characters (Table 1) were taken on 1 156 individuals of 28 populations in Japan directly from their natural habitats by the second author from 1974 to 1977 (Fig. 1, *see also* Noguchi 1986: fig. 1, table 1, and tables 18-1 and 18-2). In addition, measurements of 45 individuals from three populations in central East Korea by the second author in 1995 were included in this study. The sample size of each location, the details of habitats, and associated plants of the *Hemerocallis middendorffii* complex in Japan were described by Noguchi (1986). Voucher specimens of all collections are deposited at the herbarium of Kyoto University (KYO) and the herbarium of Gyeong-sang National University (GNUM).

For spatial autocorrelation analysis, mean values were assigned to each population for all 11 characters. In this

Table 1. List of 11 quantitative characters used in the spatial autocorrelation analysis.

Acronym	Character derivation	Unit or category
PSH	Plant (scape) height	m
LIF	Length of inflorescence minus flowers	cm
LLB	Length of the lowest bracts	cm
NFS	Number of flowers/scape	#
LPO	Length of the perianth tube enclosing an ovary	cm
LOP	Length of the outer perianth	cm
WOP	Width of the outer perianth	cm
LIP	Length of the inner perianth	cm
WIP	Width of the inner perianth	cm
LWL	Length of the widest leaf	cm
WWL	Width of the widest leaf	cm

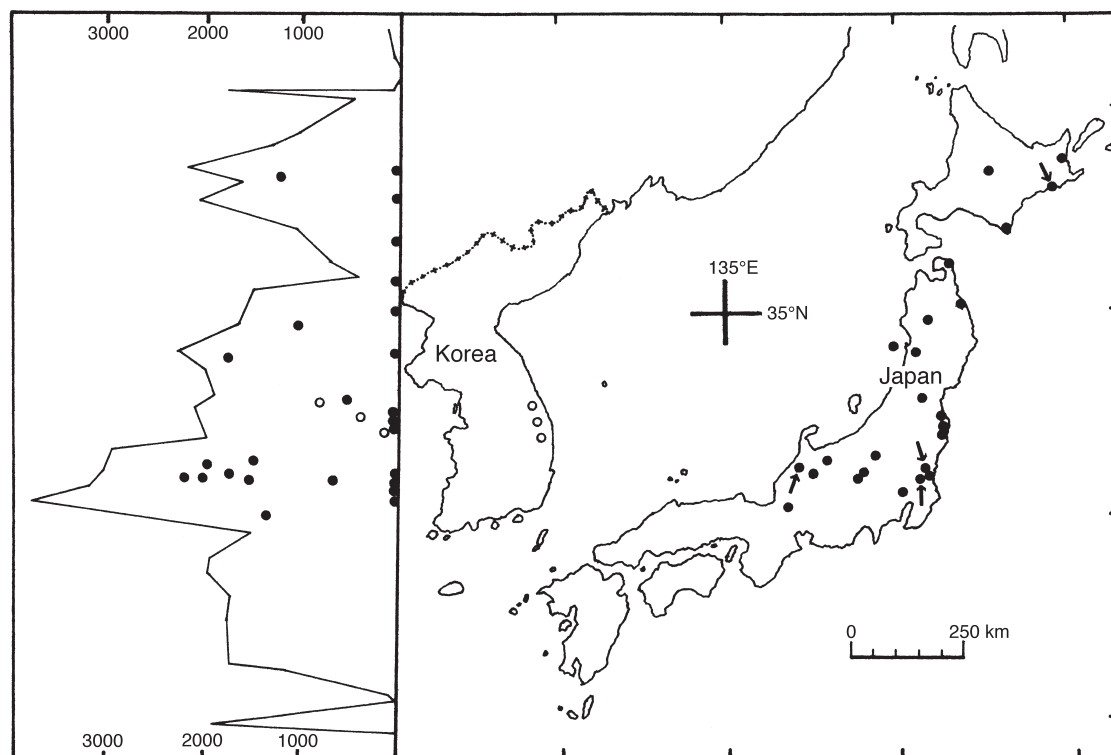


Fig. 1. The locations of the 31 examined populations of the *Hemerocallis middendorffii* complex. Open circles indicate the three Korean populations and arrows indicate that two populations were collected in each of four locations.

study, three combinations (longitude vs. latitude, longitude vs. altitude, and latitude vs. altitude) of analyses have been conducted. The approximate distance between three populations in Hokkaido is ca. 150 km. Also, the three Korean populations exhibited relatively smaller floral morphology, and the distance between populations is approximately 100 km. For these reasons, the six distance classes (the first distance is 150 km) were selected in this study. Every possible pair of populations was considered as a join and was assigned to one of six distance classes based on the geographic distance between them. These six distance classes were constructed by equalizing sample sizes among the classes. The distance classes are presented in Figs. 2 and 3. Moran's I -values were calculated for interpopulational distance classes by

$$I = N \sum_i \sum_j (W_{ij} Z_i Z_j) \left(\sum_i \sum_j W_{ij} \sum Z_i^2 \right)^{-1}$$

(Sokal & Oden 1978a). N is the number of populations, W_{ij} is the join on weighting matrix, where W_{ij} is set as one if i th and j th population are in the distance class and zero otherwise, $Z_i = X_i - X$, $Z_j = X_j - X$, the variables X_i and X_j are the mean scores for i th and j th population, respectively, and X is the mean score for all populations. The value of I ranges between +1 (complete positive autocorrelation, i.e., paired

populations have identical values for all characters) and -1 (complete negative autocorrelation). Each I -value was used to test significant deviations from the expected values, $E(I) = -1/(N-1)$ (Cliff & Ord 1981). The neighboring populations in the distance class considered, with a significant positive value of Moran's I have similar scores, whereas those with a significant negative value should have different scores. Overall significance of individual correlograms was tested using Bonferroni's criteria (Sakai & Oden 1983). All calculations and statistical analyses were performed using the SAAP program (ver. 4.3) written by D. Wartenberg.

RESULTS

Correlograms for each character of the three combinations of analysis (longitude vs. latitude, altitude vs. longitude, and altitude vs. latitude) are presented in Figs. 2 and 3. Sokal and Oden (1978a) described five correlogram patterns for geographic variation of characters. Cline is a gradual change from the highest positive I to the lowest negative I , across all distance groups. Depression is nothing

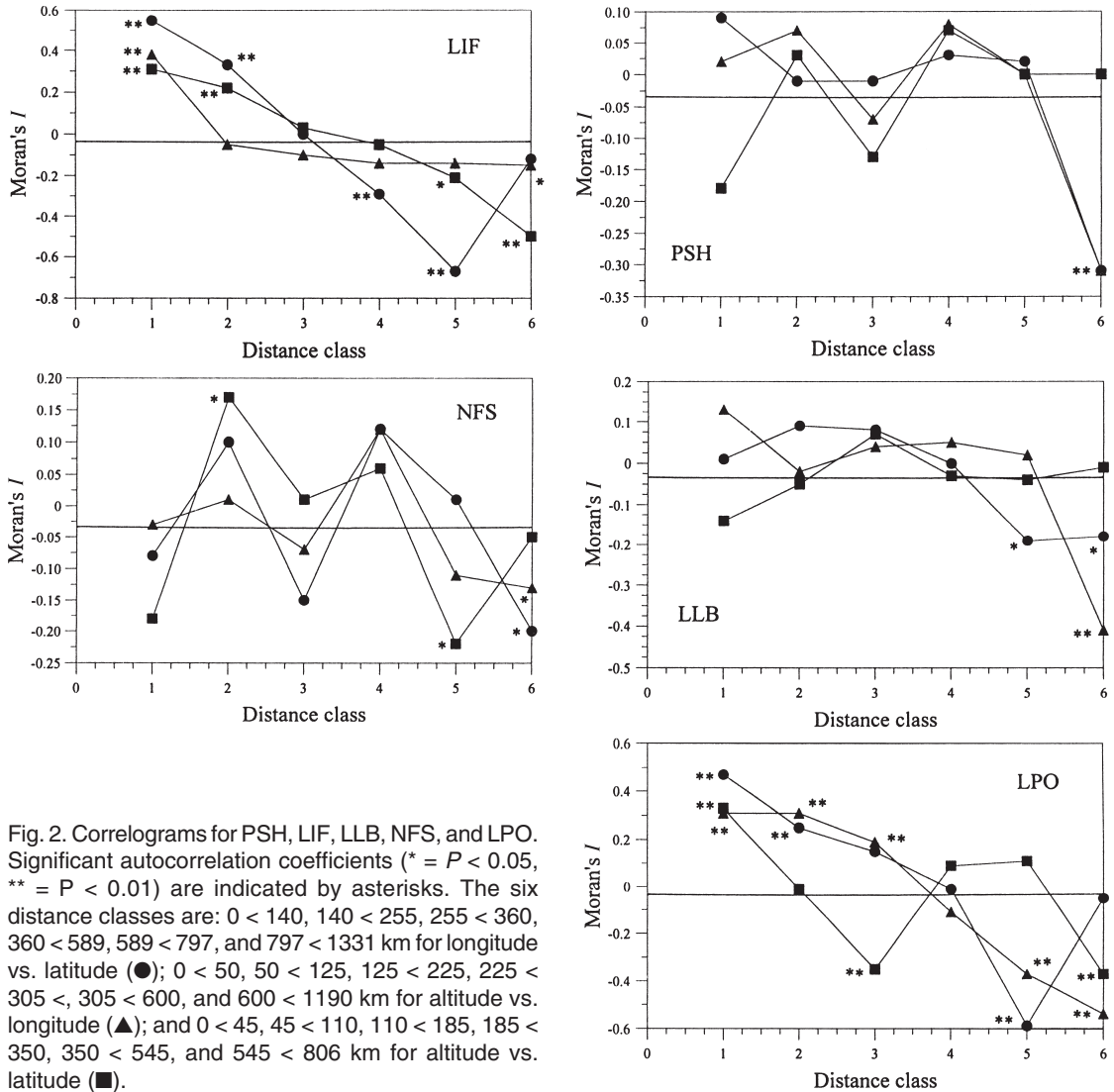


Fig. 2. Correlograms for PSH, LIF, LLB, NFS, and LPO. Significant autocorrelation coefficients ($*$ = $P < 0.05$, $**$ = $P < 0.01$) are indicated by asterisks. The six distance classes are: $0 < 140$, $140 < 255$, $255 < 360$, $360 < 589$, $589 < 797$, and $797 < 1331$ km for longitude vs. latitude (\bullet); $0 < 50$, $50 < 125$, $125 < 225$, $225 < 305$, $305 < 600$, and $600 < 1190$ km for altitude vs. longitude (\blacktriangle); and $0 < 45$, $45 < 110$, $110 < 185$, $185 < 350$, $350 < 545$, and $545 < 806$ km for altitude vs. latitude (\blacksquare).

but a circular cline, with the lowest negative I between the shortest and longest distances, not the longest distance. Double depression is on the whole quite similar to that of the depression, with low I of a certain distance from which another low I was separated. Intrusion pattern shows positive I 's at a certain distance, because of the homogeneity within the distance, with a sharply decreasing I bordering the distance. Crazy quilt pattern shows high I 's surrounded by low I 's, and vice versa, which yields no significant I 's at all. For the analysis of longitude vs. latitude, Moran's I was significant in 28 of 66 cases (42%). Only three overall correlograms (LLB = length of the lowest

bract, NFS = number of flowers per scape, and LWL = length of the widest leaf) were not significant based on Bonferroni approximation ($P > 0.10$). Correlograms for length of inflorescence (LIF) and length of the perianth tube enclosing an ovary (LPO) show depression correlograms. As with the pattern of length of inner (LIP) and outer (LOP) perianth, width of inner perianth (WIP) also show a very similar pattern as width of outer perianth (WOP), indicating that the two pairs of characters are highly correlated. A typical cline (a gradual change from the highest positive I to the lowest negative I across all distance classes) is not found in this part of analysis (Figs. 2 and 3).

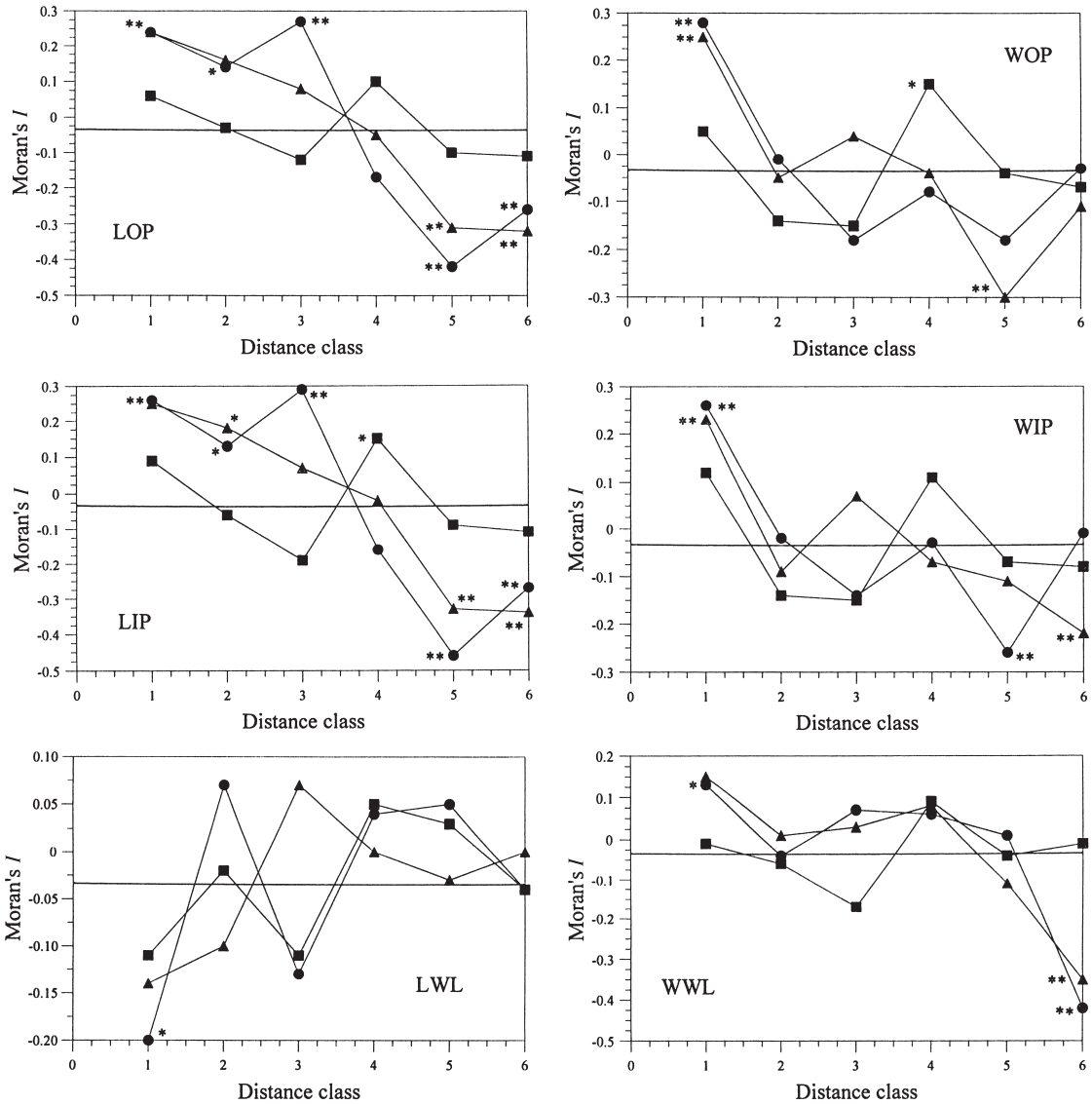


Fig. 3. Correlograms for LOP, WOP, LIP, WIP, LWL, and WWL. Significant autocorrelation coefficients ($* = P < 0.05$, $** = P < 0.01$) are indicated by asterisks. The six distance classes are: $0 < 140$, $140 < 255$, $255 < 360$, $360 < 589$, $589 < 797$, and $797 < 1331$ km for longitude vs. latitude (●); $0 < 50$, $50 < 125$, $125 < 225$, $225 < 305$, $305 < 600$, and $600 < 1190$ km for altitude vs. longitude (▲); and $0 < 45$, $45 < 110$, $110 < 185$, $185 < 350$, $350 < 545$, and $545 < 806$ km for altitude vs. latitude (■).

For the analysis of altitude vs. longitude, Moran's I was significant in 25 of 66 cases (38%). Only two overall correlograms (NFS and LWL) were not significant ($P > 0.28$). The LIF, LPO, LOP, and LIP show a clinal variation (Figs. 2 and 3). PSH vs. NFS and LLB vs. width of largest leaf (WWL) show a very similar pattern, suggesting that the pair of characters is highly correlated. The

WIP and LWL have a crazy quilt correlogram pattern with no significant autocorrelation, whereas WOP displays a depression correlogram (Fig. 3).

For the analysis of altitude vs. latitude, Moran's I was significant in 11 of 66 cases (17%). The overall correlogram for LIF (cline) and LPO (double depression) was significant ($P < 0.001$). Other correlograms show crazy quilt (PSH, LLB,

LOP, WIP, LWL, and WWL) or crazy quilt-like (NFS, WOP, and LIP) patterns (Figs. 2 and 3). Again, floral characters (LOP, WOP, LIP, and WIP) display a very similar geographic variation pattern, though WOP and LIP have an intrusion correlogram pattern (Fig. 3).

DISCUSSION

In general, there were two types of relationships between means and spatial autocorrelation observed. The first pattern of significant heterogeneity of mean with significant autocorrelation was observed for the LIF, LPO, LOP, and LIP. The second pattern of significant heterogeneity of means with weak autocorrelation is found for other seven characters. Sokal and Oden (1978b) suggested biological explanations for each of the two types of patterns. The first could result from migration via seed and pollen dispersal, founder effects, and selective agents. The second type of relationship between means and autocorrelations could result from drift, weak migration and selection, frequent local extinctions followed by the establishment of new patches by founders, or from selection in isolated, patchy environments. According to the criteria by Sokal and Oden (1978b), the crazy quilt or crazy quilt-like pattern observed for most vegetative characters (PSH, LLB, NFS, LWL, and WWL) might in part be due to phenoplasticity. Noguchi (1986) also noted that LLB, NFS, LWL, and WWL were highly variable within and among local populations, though the WWL (altitude vs. longitude) reveals a cline-like variation. Several reproductive characters (LIF, LPO, LOP, WOP, LIP, and WIP) display short distance significant-positive autocorrelations, indicating that migration and/or selective forces could be operating over these distances. A similar geographic variation pattern of the characters was observed among 30 populations of *Hemerocallis hakuunensis* Nakai, a Korean endemic species. Most floral characters show significant heterogeneity of means with significant autocorrelation, whereas most vegetative characters display significant heterogeneity of means with no significant autocorrelation. For example, perianth size (LIP, LOP, WOP, and WIP) shows significant north-south

clinal variation (Kang *et al.* 1997).

The length of inflorescence (LIF from altitude vs. latitude) shows the clearest trend of geographical cline than the other two distance combinations (Fig. 2). This, as well as means for this character per each population (Noguchi 1986) indicate that shorter inflorescences are generally located in northern, alpine, and subalpine populations, while populations with longer inflorescence occur in the lowlands of central Honshu (Noguchi 1986). The length of the perianth tube enclosing an ovary (LPO) and length of outer (LOP) and inner (LIP) perianth also display clear altitudinal and longitudinal variation, indicating that floral tubes and length of perianth in the eastern and low land populations are generally shorter and smaller than those in alpine, subalpine, and western populations. On the other hand, the width of inner (WIP) and outer (WOP) perianth show depression, crazy quilt, and crazy quilt-like variation pattern. However, these two characters in *Hemerocallis hakuunensis* show a typical monotonic decline from significant positive autocorrelation at 67 to 102 km to a significant negative autocorrelation from 21 to 357 km (Kang *et al.* 1997). The discrepancy between the two results might in part be due to extremely diverse habitats of the *H. middendorffii* complex in Japan, different distribution, and/or different adaptive mechanisms for these two characters between the two species. The correlogram for the width of the longest leaf (WWL) displays a weak geographical (altitude vs. longitude) trend. Noguchi (1986) noted that plants in alpine gravel barrens and meadows possess narrower leaves.

Although most characters of the *Hemerocallis middendorffii* complex are highly variable and the complex has been known as a taxonomically difficult group (Matsuoka & Hotta 1966, Noguchi 1986), the length of inflorescence, the length of perianth tube enclosing an ovary, and the length of inner and outer perianth showed a conspicuous geographical trend (altitude vs. longitude and/or longitude vs. altitude) in their variation pattern. Also, it should be noted that the correlograms for several floral characters, analyzed from altitudinal and longitudinal different populations show a more conspicuous geocline variation pattern, rather than those from longitude vs. latitude and altitude vs. latitude. The present results clearly

reflect the fact that the complex grows widely in East Asia and in exceedingly diverse ecological conditions from coastal grasslands up to the alpine meadows (ranging from sea level to an elevation of 2 400–2 500 m a.s.l.).

The variation pattern of several floral characters in the *Hemerocallis middendorffii* complex could be explained in terms of paleoclimatic history of the Japanese archipelago. The gradual temperature changes from warm temperature to subarctic conditions or vice versa and frequent volcanic activities during the Quaternary period have strongly influenced gene flow, size of local populations and the distribution ranges of the complex, and the ecological succession of vegetation in the Japanese archipelago and its adjacent areas. These as well as longitudinal (Sea of Japan and the Pacific Ocean), latitudinal, and altitudinal differences in the Japanese archipelago in terms of environmental pressures should have operated in the patterns of local differentiations now recognized in the *H. middendorffii* complex. It is suggested that gene flow during the Quaternary period and a possible secondary seed movement by rainfall from the mountainous areas and/or hillside to coastal areas, and selective forces or stochastic events may have played roles in the local differentiation and shaping the population genetic structure of the *H. middendorffii* complex.

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