

# Invasion of *Parthenocissus quinquefolia* (L.) Planch in the forest-steppe of Ukraine

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Received: 2 August 2022 / Accepted: 20 October 2022

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**Abstract.** Research needs of adaptation mechanisms of invasive alien species arises in connection with the naturalization of species of the genus *Parthenocissus* Planch in forest ecosystems of Ukraine. The results showed that *P. quinquefolia* has a wide range of values of edaphic and climatic factors. The populations of *P. quinquefolia* differ according to the degree of anthropogenic transformation of the ecotope, the ecological conditions formed, and the allocation of coenotics. The biomorphological characteristics of the species variability are shown on the gradient of anthropogenic transformation. Diagnostic parameters of *P. quinquefolia* under the conditions of anthropogenic transformation are the number of crotches of the tendrils and the length of the tendrils. The number of flowers per plant is characterized by the highest level of variation and belongs to the V class of variability. The smallest plasticity is characterized by the diameter of the stem. Vitality analysis indicated that cenopopulations of *P. quinquefolia* belong to the equilibria or prosperous population types, regardless of the intensity of the anthropogenic factor.

**Key words:** anthropophyte, ecological factors, biomorphology, variability, adaptation.

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## 1. Introduction

Invasion of lianoid bushes decreases richness of natural forests and disturbance of their succession (Fike & Niering, 1999; Yurkonis & Meiners, 2004). One of the most dangerous liana-like anthropophytes (according to current data, in-between epiphytes and agriophytes) are species of the genus *Parthenocissus* Planch and denized in forest ecosystems (Belousko, 2012; Berezuckiy & Haritonov, 2016). The taxonomic history, morphological and

molecular phylogenetic analysis is complex (Lu et al., 2012). *Parthenocissus* Planch. has 15 species, which are primarily located in Asia and North America; ten species in the Old World, located across East Asia; one species in West India, Sri Lanka, Java in northern Thailand; and three in North America (Krüssmann, 1989; Lu et al., 2012). The spontaneous distribution of the nonrelevant species *Parthenocissus quinquefolia* (L.) Planch has been observed in many natural areas around the world (Coladoanto, 1991; Kelbel, 2012; Vegh et al., 2015; Zajac et al., 2015, van Kleunen et al., 2018;

Burda, 2018). In countries across Europe and elsewhere, the species is given an invasive weed classification (Oviedo et al., 2012; Drake et al., 2009; Bean, 1976; Maslo, 2014; Axmacher & Sang, 2013). ‘Transformer species’ *P. quinquefolia* for the European continent should be noted among the known species of the genus *Parthenocissus*.

*P. quinquefolia* is a fast growing mesophanerophyte that reaches 7–20 m high and is capable of attaching itself to trees, poles, and other structures. The liana species is a dense tent of leaves: shading the grass, shrubs, and trees underneath. The shoots can reach a diameter of 7 cm. When pillars are absent, they crawl on the ground; thickets are formed, plants strike roots in nodes, where moisture exists, and additional roots are also formed at the internodes. Young shoots are red, tendrils reach 5–13 cm in length with 3–5 crotches, and adhesive discs result. The tips of the young tendrils are curved and later develop into shaped adhesive discs. The leaves are oval-elliptical shaped, 4–15 cm long, dark green above, bluish below, pubescent either completely or along the ribs. Petiole 5–15 cm long, glabrous. Flower buds are 2–3 mm long, with a rounded apex, and the calyx intact. The petals are elliptical 1.7–2.7 mm long, the innermost 0.6–0.8 mm long, the disk is invisible. Inflorescence, a corymb gathered in panicles with a central axis. The fruits are blue-black with 2–4 seeds (Latiff, 2012; Kozlovskiy et al., 2019). The total surface of assimilation increases and thermal radiation is reduced by up to 50%, implying that *P. quinquefolia* is a valuable taxon for wall gardening (Brice et al., 2014).

The species uses a free environmental niche due to the lack of lianoid bushes in the aboriginal flora of many European countries (Kozlovskiy et al., 2019). The plant communities of the Forest-Steppe in Ukraine have a high degree of colonization due to the anthropogenic transformation of the forests and the disturbance of the species richness of phytocenoses.

## 2. Materials and methods

To analyze the adaptive strategy of the model mesophanerophyte *P. quinquefolia*, forest biotopes were selected in the forest-Steppe area of Ukraine (Polissya-Dnipro Region, North-East-Prydniprovskaya Upland) were selected. The experimental plots (EP) were set up and differ in environmental conditions, coenosis structure, and degree of anthropogenic transformation. In total, six experimental plots were formed and six coenopopulations were analyzed. EP1- EP2 are located along the territory of the Vinnytsia forest division, the 32nd planning compartment, the 5th and 7th stratum, forest type – fresh hornbeam-oak grove (June 2016), P3 – green zone of Vinnytsia (Peoples’ Friendship Park). EP4-EP5 are located the territory of the Dakhnivsky

forest division, 11th planning compartment, forest type – fresh oak-pine grove (June 2017). EP6 – Cherkasy City Park ‘Pinewood’ (June 2018).

Conventional botanical and geobotanical methods were used in the analysis of each experimental plot (Neshataev, 1987; Mirkin et al., 2002). Plant species were determined following Dobrochaeva et al. (1987). The taxa nomenclature was adopted from Mosyakin and Fedoronchuk (1999), considering the existing ‘International Code of Nomenclature for Algal, Fungi, and Plant’ (McNeill, 2011). Changes in ecological conditions were detected by the ecological structure of the grass layer, using the appropriate scales (Didukh & Pluta, 1994). Processing and the calculation of amplitudes of edaphic factors were performed by syn-phytoindicative method using ECODID programme. The state of the soil surface layer was determined according to Polyakov and Plugatar (2009) and represented according to the following categories: 1 – undisturbed soil; 2 – weakened mulch (single passes); 3 – footpath in mulch; 4 – footpath or road without mulch; 5 – footpath or road with washaways; 6 – deposition and washouts made by recreants descending on steep slopes. The stages of digression of soil surface layer were the following: I – under which the 3rd, 4th, 5th and 6th categories of disturbance cover up to 2% of the area of the experimental plot; II – from 2% to 10% of the area; III – 10% – 25% of the area; IV – 26% – 40% of the area; V – over 40% of the site area.

The health condition of trees (category of tree condition) was appraised following the Sanitary Forest Regulation in Ukraine (2016). The stand state index was calculated as the sum of the tree state index within a specified category divided by the total number of examined trees.

$$I_c = \frac{\sum k_i \cdot n_i}{N}, \quad (1)$$

where  $k_i$  is the category of the tree state (I–VI);  $n_i$  is the number of trees in a certain category of the tree state and  $N$  is the total number of trees.

Stands with index values ranging from 1 to 1.5 are considered as healthy (I), 1.51–2.50 as weaker ones (II), 2.51–3.50 as heavily weakened ones (III), 3.51–4.50 as wilting ones (IV), 4.51–5.50 as recently dead (V) and 5.51–6.50 old dead stands (VI). The stages of the recreational transformation were assessed according to Rusin (2003) (Table S1 in Annex).

Evaluation of morphometric parameters of populations of the model species *P. quinquefolia* was performed following Zlobin (2009). The subjects of the biometric tests were: plant height ( $h$ , m), the number of flowers per plant ( $N_{Fl}$ , pcs.), stem diameter ( $d$ , mm), length of tendrils ( $L_m$ , cm), the number of crotches of tendrils ( $N_{mr}$ , pcs.), leaf length

( $L_j$ , cm), leaf width ( $W_j$ , cm), inflorescence length ( $L_s$ , cm) (Table S2). A sample size of 50–75 individuals was selected from each population. The coefficient of variance was used to estimate the variability of the characteristics (CV, %). The following limits were established to identify the degree of variability of characteristics according to Lakin (1990):  $V > 25\%$  – high;  $V = 11–25\%$  – average;  $V < 10\%$  – low. Vitality analysis was performed to assess the state of the population using a one-dimensional approach according to standard methods (Zlobin, 2009). The population quality index (Q) was determined as:

$$Q = 0,5 \times (a+b) \quad (2)$$

where  $a$  is the number of individuals in the first vitality class, and  $b$  is the number of individuals in the middle vitality class. The population is considered prosperous when  $Q > c$ , equilibrium when  $Q \approx c$  and depressed when  $Q < c$ . Ecological plasticity and stability of the species were calculated following Eberhart and Russell (1966).

To assess the morphological integrity of plants, we used the morphological integrity index according to Zlobin (2009):

$$IMI = \frac{B}{(n^2 - n) / 2} \times 100 \quad (3)$$

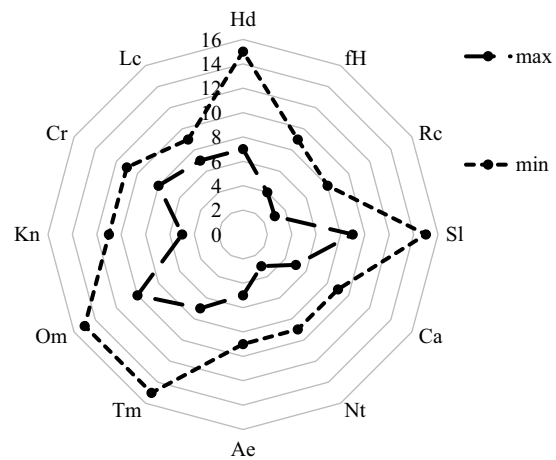
where IMI is the index of morphological integrity; B is the number of statistically significant correlation coefficients (p-value 0.95) correlation coefficients in the matrix; n is the total number of estimated morphometric parameters.

Correlation analysis using the Spearman correlation coefficient (Pearson) was used to identify the coherence between the morphometric features.

### 3. Results

Analysis of environmental factors showed that the species has a wide range of values of both edaphic and climatic factors (Fig. 1). In relation to the cryogenic regime, the species is a frost tolerant, heminostenotopic subcryophyte. Continentality, subcontinental hemievrytop, ombro mode – subombrophytic hemistenotop. According to the characteristics of edafotop, the introduced species perfectly adapts to changes in nitrate, acid (hemistenotopic subacidophile) and salt regimes of the soil. In relation to the hydrological regime, the species is a hemistenotopic mesophyte, in terms of moisture variability – a hemievrytopic hemihydrocontrastophile. In relation to soil aeration, *P. quinquefolia* is a hemistenotopic hemiaerophobic plant, a plant of moderately aerated soils with terminable groundwater moistening. Luminance and soil trophicity are the limiting edaphic factors.

In EP1 and EP2 the first tier is represented by *Quercus robur* L. (60–80 years old) and *Tillia cordata* Mill. (40–60 years old). The second tier stand (40–50 years) is dominated by *Carpinus betulus* L. with the presence of *Acer platanoides* L. and *Fraxinus excelsior* L. The undergrowth is represented by *Q. robur*, *A. platanoides*, *F. excelsior*, *T. cordata*. The underbrush is dominated by *Euonymus europaea* L., *Euonymus verrucosa* Scop., *Sambucus nigra* L., *Corylus avellana* L. On EP1 the canopy density is 0.8–0.9, on EP2 it is 0.8–0.7. In EP1, disturbed soil areas (5.5 percent) are represented by litter paths and single passages, the area is not fouled. The development of *P. quinquefolia* on EP1 was recorded at three open loci, the species crawls on the soil surface and rises on the trunks of trees of the 1st and 2nd tiers. In some places *P. quinquefolia* can be seen even in the crowns of *C. betulus*, *A. platanoides* and *F. excelsior*. The total area of the sinuses is 35 m<sup>2</sup>. The lifespan of the liana is high. The general condition of the stand is 1.53. The total plant cover of the grass layer is 85 percent. Typical forest species *Aegopodium podagraria* L., *Carex pilosa* Scop., *Allium ursinum* L., *Asarum europaeum* L., *Brachypodium sylvaticum* (Huds.) P.Beauv., *Convallaria majalis* L., *Dryopteris filix-mas* (L.) Schott, *Ficaria verna* Huds, *Galium odoratum* (L.) Scop., *Geranium robertianum* L., *Mycelis muralis* (L.) Dumort., *Polygonatum multiflorum* (L.) All., *Pulmonaria obscura* Dumort., *Scilla bifolia* L., *Stellaria holostea* L., *Viola odorata* L. etc. dominate. Only in some places, there are ruderal species, among which *Urtica dioica* L., *Impatiens parviflora* DC., *Stachys annua* L. and others should be noted. Out of the environmental threats, recreational load and insignificant mechanical impact on the biota due to the collection of medicinal herbs, berries, and mushrooms were observed. The degree of anthropogenic transformation of the ecotope was II.



**Figure 1.** Range of indicators' values of ecological factors of *P. quinquefolia* (Rc – soil acidity, Tr – salt regime of the soil, Nt – available soil nitrogen, Hd – soil moisture, Ca – soil carbonate, Tm – thermal regime of climate, Kn – continentality of climate, Cr – climate cryoregime)

On EP2 the share of disturbed soil areas was slightly higher – 11.2 percent, but the categories remain the same as on EP1, areas with soil erosion were not recorded. The general condition of the stand has deteriorated and was 1.75. The development of *P. quinquefolia* on EP2 was recorded at five open loci, the species spreads both on the ground and climb up on tree trunks. *P. quinquefolia* is present in the crowns of *C. betulus*, *A. platanoides*, *F. excelsior* to a greater extent than on EP1. It should also be noted that the death of lower-order scaffold branches wrapped in lianas was observed in seven individuals of *C. betulus* and nine individuals of *A. platanoides*, which may be associated with impaired photosynthesis in tree leaves. The total area of sinuses was 90 m<sup>2</sup>. The vital power of the liana was high. The total plant cover of the grass layer was 55.0 percent, the community includes forest species that dominate EP1, but their cover is significantly fewer. At the same time, among the unconventional species *Ambrosia artemisiifolia* L., *Dactylis glomerata* L., *S. annua*, *Plantago major* L., *Chelidonium majus* L. should be noted. Among the environmental threats the recreational load, proximity to the transport network, the presence of unorganized recreation areas, collection of medicinal herbs, fungi, etc. were detected. The degree of anthropogenic transformation was II.

EP3 is located in the urban ecosystem of Vinnytsia, People's Friendship Park, the stand consists of two tiers; the first is represented by many species, among which *Q. robur*, *Quercus rubra* L., *C. betulus*, *A. platanoides*, *T. cordata*, *Pinus nigra* Arnold. dominate, in the second tier *Betula pendula* Roth, *Salix alba* L., *Aesculus hippocastanum* L., *Abies alba* Mill., *Pinus sylvestris* L., *Robinia pseudoacacia* L. were registered. In the underbrush, *Sorbus aucuparia* L., *Crataegus laevigata* (Poir.) DC., *Viburnum opulus* L., *Malus sylvestris* Mill., *Syringa vulgaris* L. should be noted. Plantations alternate with open lawns with miscellaneous plants. Disturbed soil areas occupy 15 percent of the territory, mainly comprised of trails. Stage of recreational soil digression – 2. The general condition of the stand was 2.15. The development of *P. quinquefolia* in the city park was recorded at 11 loci. *P. quinquefolia* rises to a height of 10–12 m, penetrating the crowns of the trees. It should be noted that in the undergrowth the species envelops almost 70 percent of the tree stems of *F. excelsior*, *A. platanoides*, *A. negundo*, *B. pendula*, *S. alba*, *M. sylvestris*, *S. vulgaris* and others. In 23.5 percent of small trees mantled with lianas, the lower branches either wither or die. Liana is widespread in many places, forming monodominant plantations, gradually becoming a subedificator of the grass layer with a plant cover up to 68 percent. The total area of sinuses was 175 m<sup>2</sup>. The vital power of the liana was high. The total plant cover of the grass layer is 65.0 percent, the community is dominated by *Leucanthemum vulgare* L., *Achillea millefolium*

L., *A. artemisiifolia*, *D. glomerata*, *Hypericum perforatum* L., *S. annua* etc. Observations of the grass layer showed that forest species were underrepresented. Among the environmental threats recreational load, urbanization, transport, municipal waste was observed. The degree of anthropogenic transformation is IV.

On EP4 and EP5, the first tier is represented by *P. sylvestris* (60–80 years old), the second tier is represented by *Q. robur* (60–80 years old). In undergrowth germinate *Q. robur*, *A. platanoides*, *A. negundo*. The underbrush is dominated by *E. europaea*, *E. verrucosa*, *S. nigra*, *Sambucus racemosa* L. On EP4 the canopy density is 0.7–0.8, while on EP5 it is 0.7–0.6. On EP4 characteristic species for this forest type dominate in the grass layer (total plant cover was 84 percent), among violents, *G. robertianum*, *Viola tricolor* L., *Betonica officinalis* L., *S. holostea*, *A. millefolium*, *Galium aparine* L. etc. should be noted. *I. parviflora*, *S. annua*, *U. dioica*, *A. artemisiifolia* occur along paths and passages. Disturbed soil areas, trails in the litter, and single passages occupy 8.0, 5.5, and 2.5 percent, respectively. The overall sanitary condition of the stand was 1.62. The occurrence of *P. quinquefolia* on EP4 was recorded at five small loci, the species rises along the trunks of *Q. robur* and *P. sylvestris*, and does not penetrate the crown. The total area of sinuses was 29 m<sup>2</sup>. The condition of the liana is average. Recreational stress and insignificant mechanical impact on biota were recorded among environmental threats. The degree of anthropogenic transformation is III.

EP5 is located closer to urban ecosystems, increasing the probability of damaged trees and soil surface. The general condition of the tree stand was 1.73. Undisturbed soil surface – 64 percent. Three fire pits and three small dumps were observed in the trampled meadows. The development of *P. quinquefolia* on EP5 was recorded at six loci. In areas where the introduced species is monodominant, the undergrowth was completely covered with *P. quinquefolia* 84 percent with significant damage to the grass layer. On loci with *P. quinquefolia*, only *Anthriscus sylvestris* (L.) Hoffm., *C. majus* and *Geum urbanum* L. develop in the grass cover. The introduced species grows not only in height, but along the branches on the crown of the trees of *A. platanoides*, *A. negundo*, *S. nigra* and *S. racemosa*. The total area of sinuses was 101.5 m<sup>2</sup>. The vital power of the liana was high. The total plant cover of the grass layer was 60.0 percent, the community includes forest and synanthropic species. The ecological threats for EP5 included: recreational load; proximity to the transport network and urban ecosystems; presence of unorganized recreation areas; collection of medicinal herbs; fungi; etc. The degree of anthropogenic transformation was II.

EP6 is located in the City Park 'Pinewood' in Cherkasy. This EP has significant consequences of negative anthropogenic impact on the environment. The condition

of pine plantations – severely weakened (2.58). The underbrush is poorly developed and undergrowth was dominated by atypical edificatory species – *A. platanoides* and *A. negundo*. The canopy density was 0.5. Significant soil trampling was revealed, damaged areas accounted for 43 percent, 10 percent were roads and trails with erosion. The share of adventitious and ruderal species was 75 percent (*A. artemisiifolia*, *Eragrostis minor* Host, *I. parviflora*, *Lactuca serriola* L., *U. dioica*, *C. majus*, etc.), among typical forest species only *G. robertianum*, *S. holostea* and *Rubus nessensis* Hall occurs singly. The development of *P. quinquefolia* in the park was recorded at 17 loci. The species rises to a height of 14 m, penetrating the canopies. In addition to the undergrowth, which is almost completely wrapped at 80 percent of its height, penetrating trees crowns of the 1st and 2nd tiers of *P. sylvestris* and *Q. robur*. The plant cover of the mesophanerophyte reaches 75 percent. The total area of sinuses is 202 m<sup>2</sup>. The vital power of the liana was high. The degree of anthropogenic transformation was III.

Assessment of habitats and analysis of the intensity of impact of environmental threats revealed the degree of anthropogenic transformation of the ecotope and the ranking of EP by the gradient of the corresponding changes in environmental conditions (Table S3). The anthropogenic transformation degree of the ecotope formed during various ecological conditions and coenotic allocation distinguishes the studied populations from the invasive alien species.

#### Biomorphological characteristics of species variability on the gradient of anthropogenic factor

The violation of habitat conditions, changes in edaphic conditions, luminance, where common among the studied coenopopulations. Characteristic values of the morphometric parameters varied depending on environmental factors and the gradient of anthropogenic impact. In particular, the height of the *P. quinquefolia* shoot varied from min  $8.6 \pm 0.43$

m (EP4) to max  $19.0 \pm 0.95$  m (EP6) (Table 1). EP3 and EP6 were among the tallest with a strong level of anthropogenic transformation. A similar trend was identified when the change in the diameter of the shoot was considered. (e.g. higher the plant, larger its diameter). The values of the morphometric parameter (Table 1) values for EP1-EP2 and EP3-EP4 were within a similar range. The parameters values for the number of crotches of tendrils and length of tendrils were the least variable; the correlation between the change in values on the gradient of anthropogenic transformation and the change of environmental factors was not revealed. These parameters are the most stable fractions for the coenopopulations of *P. quinquefolia* studied, which can be considered diagnostic for the species under anthropogenic transformation conditions. The quantity of studied generative organs (number of flowers) varied from  $34 \pm 1.7$  pcs (EP4) to  $79 \pm 3.9$  pcs (EP6). An interesting trend was observed in the variation of the number of inflorescence lengths. This indicator is a variable fraction where the highest values are characteristic of coenopopulations EP3, EP4 and EP6 with the highest transformation level. Analysis of the morphometric parameters of the leaves showed variation in the data with vegetative parameters varying widely in different coenopopulations. The smallest leaf width was recorded for the coenopopulation EP6 ( $5.3 \pm 0.3$  cm), the largest – for EP3 ( $13.0 \pm 0.7$  cm).

A close correlation was identified between plant length and its diameter (0.97), leaf length (0.94), and inflorescence length (0.95) (Table 2), the correlation between leaf height and diameter was slightly weaker (0.79). The correlation between these quantitative features was no longer recorded at probability values. A strong correlation for the number of flowers per plant parameter is observed with inflorescence length (0.88). The relationship between shoot diameter, tendril length, and the number of branches was found to be rather interesting. The number of tendrils and their branches are correlated. The length of the leaves was related

**Table 1.** Morphometric parameters of *P. quinquefolia*

	1				2				3				4				5				6			
	M	min	max	SD	M	min	max	SD	M	min	max	SD	M	min	max	SD	M	min	max	SD	M	min	max	SD
h, m	12.3	9.2	15.7	2.4	11.8	8.7	16.3	3.2	15.8	11.8	17.4	1.9	11.1	8.6	13.7	1.1	11.0	8.8	14.2	1.9	17.6	14.3	19.0	2.0
N <sub>Fl</sub> , pcs.	54	38	65	15	51	41	69	19	55	50	76	22	58	34	76	23	45	40	61	11	68	43	79	25
d, mm	2.2	1.5	3.2	0.8	2.0	1.3	3.4	0.7	2.7	2.0	4.1	1.0	2.8	1.5	3.8	0.7	2.3	1.6	3.9	0.8	3.0	2.4	4.3	1.1
L <sub>m</sub> , cm	6.4	5.0	10.2	1.1	6.3	4.7	8.5	0.9	6.9	5.5	9.0	1.3	5.9	5.4	8.1	0.9	5.8	5.6	8.9	1.1	6.8	5.7	10.6	1.3
N <sub>mr</sub> , pcs.	3.8	3.0	5.0	0.8	3.6	3.0	5.0	0.7	3.9	3.0	5.0	0.8	3.4	3.0	5.0	0.7	3.5	3.0	5.0	0.8	4.0	3.0	6.0	0.9
L <sub>l</sub> , cm	7.8	5.4	10.2	1.9	8.0	6.1	11.2	1.9	9.1	6.5	13.0	2.1	7.2	5.6	9.3	1.8	7.0	4.5	9.0	1.8	9.6	5.3	12.9	2.0
W <sub>l</sub> , cm	5.5	5.1	6.2	0.3	5.4	5.2	6.3	0.3	6.5	5.3	7.1	0.4	5.4	5.0	6.5	0.2	5.2	5.0	5.8	0.3	6.6	5.4	6.9	0.3
L <sub>s</sub> , cm	9.4	8.7	12.3	1.9	9.3	8.4	12.5	2.2	10.1	9.1	15.3	3.1	9.6	8.7	13.2	2.1	9.3	8.5	14.1	3.0	11.3	9.0	14.5	2.7

Note: SD – standard deviation, plant height (h, m), the number of flowers per plant (N<sub>Fl</sub>, pcs.), stem diameter (d, mm), length of tendrils (L<sub>m</sub>, cm), the number of crotches of tendrils (N<sub>mr</sub>, pcs.), leaf length (L<sub>l</sub>, cm), leaf width (W<sub>l</sub>, cm), inflorescence length (L<sub>s</sub>, cm).

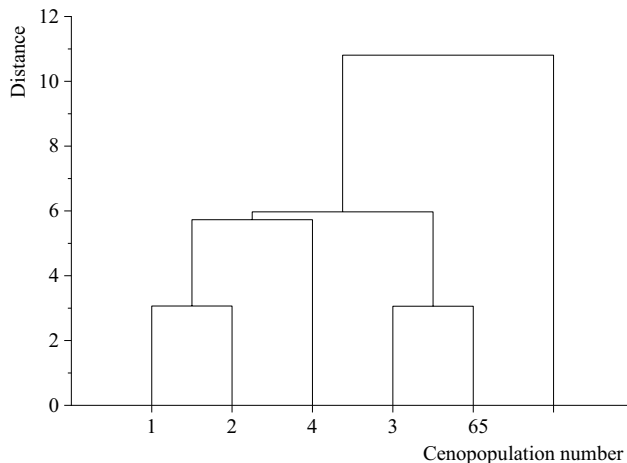
to the width of the leaves and the length of the inflorescence. However, there is no close bond between leaf width and inflorescence length.

**Table 2.** Correlation between morphometric parameters of *P. quinquefolia*

h	0							
N <sub>Fl</sub>	0.05	0						
d	0.97	-0.28	0					
L <sub>m</sub>	0.95	0.04	0.76	0				
N <sub>mr</sub>	-0.01	-0.32	0.71	0.97	0			
L <sub>l</sub>	0.94	-0.01	0.08	-0.56	0.13	0		
W <sub>l</sub>	0.79	0.11	-0.04	-0.33	-0.17	0.82	0	
L <sub>s</sub>	0.74	0.88	-0.43	0.27	-0.58	0.76	0.35	0
	h	N <sub>Fl</sub>	d	L <sub>m</sub>	N <sub>mr</sub>	L <sub>l</sub>	W <sub>l</sub>	L <sub>s</sub>

Note: plant height (h, m), the number of flowers per plant (N<sub>Fl</sub>, pcs.), stem diameter (d, mm), length of tendrils (L<sub>m</sub>, cm), the number of crotches of tendrils (N<sub>mr</sub>, pcs.), leaf length (L<sub>l</sub>, cm), leaf width (W<sub>l</sub>, cm), inflorescence length (L<sub>s</sub>, cm).

Based on the analysis of the dendrogram 'similarities-differences' of the morphometric parameters, two main groups of clusters stood out (Fig. 2). The features of 3 and 6 cenopopulations, as well as 1 and 2 cenopopulations, were the most similar. The slightest signs of similarity with other coenopopulations were found for individuals in the 5 coenopopulation.



**Figure 2.** Dendrogram of morphometric parameters of *P. quinquefolia*

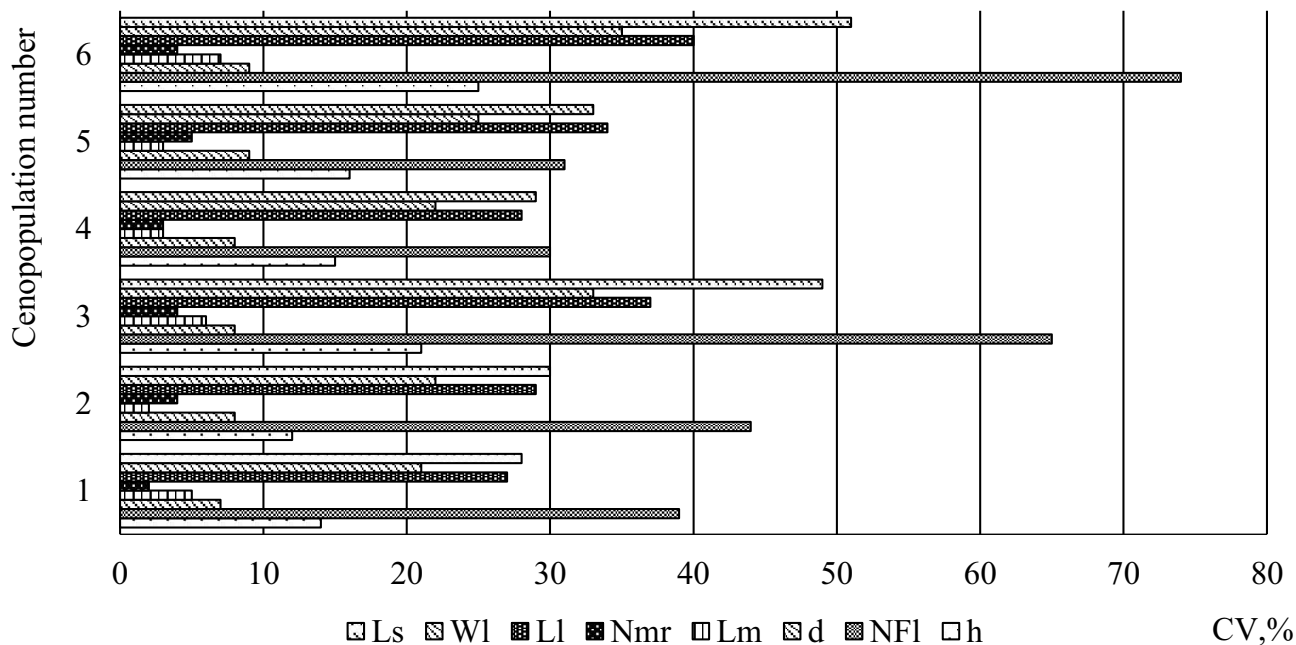
Analysis of the impact of changes in environmental factors shows that the invasive alien species quickly adapt to changing conditions, responds to acidity, aeration and moisture of the soil and the luminance degree under the canopy. This is indicated by the dependence of the height of individuals along the gradient of factors considered (Fig. S1a,

b in Annex). Among the parameters analyzed, the height of the plant was chosen as the model fraction, due to the high correlation and variability of the characteristic. In particular, it was found that *P. quinquefolia* adapts well to changes in soil acidity from acidic to neutral, with increases in levels of anthropogenic transformation and approaches of pH to sub-acidic (Fig. S1a). The evaluation of the influence of the soil hydrological regime showed that the species tolerates a wide range of hydrological soil conditions but performs better under conditions of xerophytization, as evident by the dependence of plant height on the soil hydrological regime (Fig. S1b). The same tendency also remains for the dependence of plant height on other environmental factors of the soil (Fig. S2).

Examination of the dependence of the reproductive fractions when the quantity of flowers showed a strong correlation ( $R = 0.84$ ,  $p = 0.005$ ) with the luminance regime of the soil. The number in flowers of the plant increases in direct proportion to the increase in luminance. This dependence was inversely proportional to the length of the inflorescence ( $R = -0.76$ ). The evaluation of the variability of the morphometric parameters showed that the quantity of flowers is characterized by a high level of variation and belongs to the Vth high class of variability (Fig. 3). It should be noted that CV increases along the transformation gradient, with increasing intensity of anthropogenic impact, and the CV share increases from 30–44 percent and 65–74 percent.

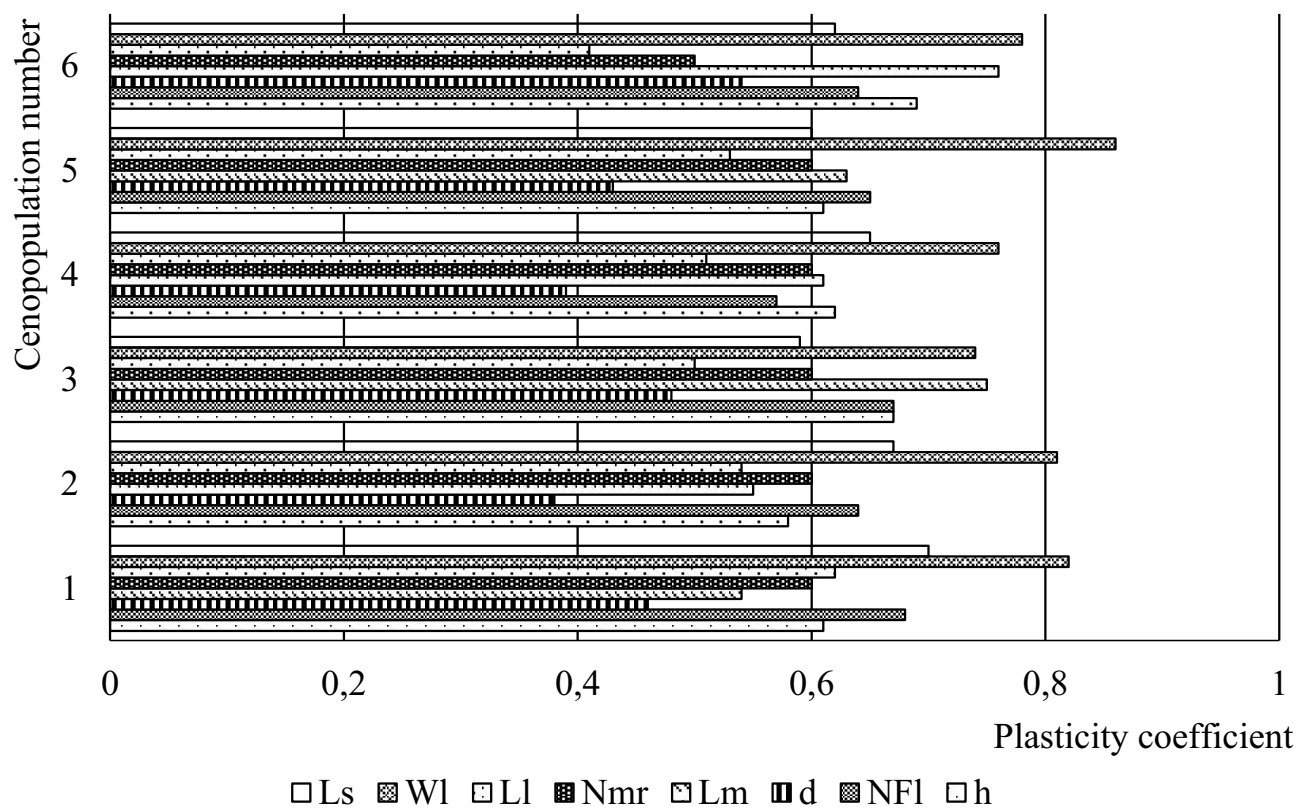
The parameters inflorescence length, leaf width, leaf length are somewhat more stable. The variability level of these characteristics belongs to the IVth class. At the same time, the variation of leaf parameters depends less on the intensity of anthropogenic impact compared to inflorescence length. The low variation level (class II) includes the shoot characteristics (height and diameter). However, only height variability increases on the transformation gradient from 14 to 25 percent. No significant increase in diameter variation was detected in coenopopulations. The parameters length of tendrils and the number of crotches of tendrils, were most stable, when characterized by the lowest variation level. The plasticity of the trait was analyzed as a variation of mean values along the gradient of living conditions, the results indicated that the morphometric parameters are low- and highly plastic (Fig. 4). The number of flowers per plant, leaf width, and inflorescence length are characterized by high plasticity. Slightly lower values are inherent in plant height, length of tendrils, and leaf length. The diameter of the plant and the number of branches of the tendrils are characterized by low levels of plasticity.

Following the results of the vitality analysis, all studied coenopopulations belong to the prosperous type, two coenopopulations are equilibria – EP1 and EP4 (Table 3). The



Note: plant height (h, m), the number of flowers per plant ( $N_{Fl}$ , pcs.), stem diameter (d, mm), length of tendrils ( $L_m$ , cm), the number of crotches of tendrils ( $N_{mr}$ , pcs.), leaf length ( $L_l$ , cm), leaf width ( $W_l$ , cm), inflorescence length ( $L_s$ , cm)

Figure 3. The coefficients of variation of morphometric parameters of *P. quinquefolia*



Note: plant height (h, m), the number of flowers per plant ( $N_{Fl}$ , pcs.), stem diameter (d, mm), length of tendrils ( $L_m$ , cm), the number of crotches of tendrils ( $N_{mr}$ , pcs.), leaf length ( $L_l$ , cm), leaf width ( $W_l$ , cm), inflorescence length ( $L_s$ , cm)

Figure 4. The values of the plasticity coefficient of morphometric parameters of *P. quinquefolia*

highest values of the quality index have cenopopulations 3 and 6, characterized by high abundance rates of individuals with intense exposure to environmental threats. It is worth mentioning that the share of c-class individuals is only 5 percent on EP3. Cenopopulations 1 and 4 were characterized by the lowest values of the quality index. IMI values range from 0.63 for population 1 and up to 0.80 for population 3, indicating a generally high level of morphological integration of *P. quinquefolia* individuals.

**Table 3.** Vitality composition of *P. quinquefolia* cenopopulations by the gradient of anthropogenic transformation

Cenopopulation number	IMI	The share of plants by vitality classes			Quality index Q	Population type	Transformation stage
		a	b	c			
1	0.63	0.41	0.29	0.30	0.350	equilibril	II
3	0.68	0.55	0.28	0.17	0.415	prosperous	II
2	0.78	0.68	0.27	0.05	0.475	prosperous	IV
5	0.65	0.34	0.38	0.28	0.360	equilibril	III
4	0.69	0.49	0.27	0.24	0.380	prosperous	II
6	0.72	0.57	0.31	0.12	0.440	prosperous	III

#### 4. Discussion

In the conditions studied in the Forest-Steppe of Ukraine, the introduced species is a subedificator of the forest grass layer, displaces typical forest species, and large stable sinuses are formed. Other researchers emphasize that *P. quinquefolia* is found in man-made habitats such as, urban railway embankments, old walls and buildings, and road verges. Scrub and hedgerows are also invaded (Pilkington, 2011). Parks play an important role in spreading, as it is for *P. quinquefolia* planted in private gardens (Pergl et al., 2016). For these types of invasive plants, spreading occurs randomly causing both ecological and maintenance-oriented issues in gardens and public parks (Vegh et al., 2015).

Examination of both the fundamental and realized ecological niches of *P. quinquefolia* showed that the primary climatic limiting factor is the ambient temperature. The optimum temperature during the growing season is in the range of 28–32°C. At temperatures above 36°C, the assimilation of carbohydrates by the leaves is reduced, catabolism is intensified, resulting in a delay in berry ripening (Brice et al., 2014). *P. quinquefolia* is more prone to xerophytic conditions, a result of a loss of a portion of the minerals needed for assimilation when soil moisture increases. Therefore, growth is delayed along with the development of the generative organs of the species (Ward et al., 2020). According to the estimation of edaphic factors,

a wide range of soils is the most optimal: from sandy to loamy. *P. quinquefolia* is a salt-resistant species. Other authors note that the populations of *P. quinquefolia* flourish in nutrient-rich soils. Due to its rapid growth *P. quinquefolia* displaces natural herbaceous plants from the forest ecosystem (Branquart et al., 2011). A forthcoming study confirmed this result.

Invasive alien species quickly adapt to changing environmental conditions, responds to acidity, aeration and moisture of the soil, and the luminance degree under the canopy. According to the literature (Dickens, 2015; GRIIS, 2020), the introduced species is shade-tolerant, but our research has shown that the species gravitate more toward semi-open areas.

Studies at the complex population level of the invasive alien species *P. quinquefolia* revealed its adaptive strategy: identifying the bond between intra-population variability and the adaptive capacity of the species. *P. quinquefolia* is a very aggressive adventitious species, competing not only for resources with herbaceous plants, but also penetration of canopy space (Kelbel, 2012).

According to the literature, indices of biological characteristics of reproduction of *P. quinquefolia* (crop yield, seed viability, germination capacity), aptitude for spontaneous spreading (ground-space and number of plants, seedling density under the mother plant), and maturation (coloration, shedding and soluble dry weight of fruits) have higher rates. Researchers found a positive correlation exists between the invasion capacity and the number of seedlings, fruits, and germination capacity of seeds (Vegh et al., 2015). *P. quinquefolia* reduced stem biomass when grown with other species, and root biomass was not affected by competition. The results suggest *P. quinquefolia* is likely a strong competitor (Emerine et al., 2013). *P. quinquefolia* adapts well to drought-resistant conditions when the growth rate and photosynthetic response to water are considered, suggesting that this species could be resilient to water availability (Zhang et al., 2004).

Our study analyzed the correlation between the variability of morphometric parameters and changes in ambient edaphic conditions. The comparative characteristics of both fundamental and implemented ecological niches and biomorphological parameters of species *P. quinquefolia* variability on the gradient of increasing anthropogenic factors can be used as an ecosystem bioindicator.

#### 5. Conclusion

The results of our study have shown that invasive alien species are best characterized by increased tolerance to changes in abiotic environmental factors. This is due to the adaptation



mechanism and the expansion of the realized ecological niche when viewed as a consequence of the capture of new ecotopes. Based on our study, invasive alien species defined as eurybiont by soil regimes in habitats, along the gradient, weaken their condition and development, and are dependent on the variability of factors' influence time and space; most notably anthropogenic and abiotic.

### Acknowledgements

This work was supported by the National University of Life and Environmental Sciences of Ukraine, grant number 0117U002647.

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