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A comparison of the Southern Appalachian (U.S.A.) and Southwestern Caucasus (Russia) forests: influences of historical events and present environment

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Abstract. The Southern Appalachian (North America) and Southwestern Caucasus (Eastern Europe) forests have a common origin, the warm-termperate Tertiary forests, but a different history of development. The Southwestern Caucasus forests experienced a dramatic species loss at the end of the Tertiary, while the Tertiary flora of the Appalachian region was preserved without major changes. Certain similarities and differences between the flora and vegetation of the Southern Appalachians and Southwestern Caucasus can be attributed to the Tertiary and post-Tertiary history of both regions. The similarities include the species-to-genus and species-to-families ratios and the floristic composition. The differences include taxonomic diversity and percentage of tree taxa.

Key words. Warm-temperate forests, historical events, present environment.

The present-day geographic distribution of plant taxa is a product of the interaction between the numerous geomorphologic, climatic, and biological processes at a variety of spatial and temporal scales (Szafer, 1975; Collinson, 1988; Delcourt & Delcourt, 1991). Consequently, it is argued that some patterns of species diversity in plant communities cannot be correctly interpreted without referring to the origin and subsequent development of these communities (Chesson & Case, 1986; Davis, 1986). Certain attributes of the contemporary vegetation, such as species richness, are related in part to the current environment and in part to historical events. For example, the increase in species richness from the temperate zone to the tropics has been attributed to combination of modern climate and resources (Grubb, 1987). At the same time, a significant difference in the number of tree genera between Europe and North America is considered to be the result of the Pleistocene extinctions, and is not directly related to the present environmental conditions of both continents (Grubb, 1987; Delcourt & Delcourt, 1991). In general, floristic and vegetation patterns that cannot be explained by the contemporary environmental conditions are often the outcome of such historical processes as speciation and extinction, which are driven or enhanced by various climatic and geomorphologic events. Identifying these patterns at various spatial scales helps to understand the mechanisms that create and maintain the diversity of the world's flora and vegetation.

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This study evaluates the influence of historical events and present environmental conditions on the regional floras of the Southern Appalachians (North America) and the Southwestern Caucasus (Eastern Europe) with a particular emphasis on the forest communities (Fig. 1). These communities share a common floristic origin in the northern hemisphere, warm-temperate Tertiary forests, but subsequently they have had a different history of development (Grossgeim, 1948; Braun, 1964; Tallis, 1991).

The role of historical factors and present environment was evaluated with respect to the following features of the Southern Appalachian and Southwestern Caucasus plant cover:

taxonomic richness at the level of species, genera and families;
percentage of tree shrub, herbaceous and vine growth forms;
percentage of endemic species;
similarity between the floras (families of vascular plants and arborescent genera);
species-to-families and species-to-genus ratios;
habitat preferences of monodominant forest community types.

REGIONS OF STUDY

Southern Appalachians

The region of study within the Southern Appalachians corresponds to the southern section of the Blue Ridge

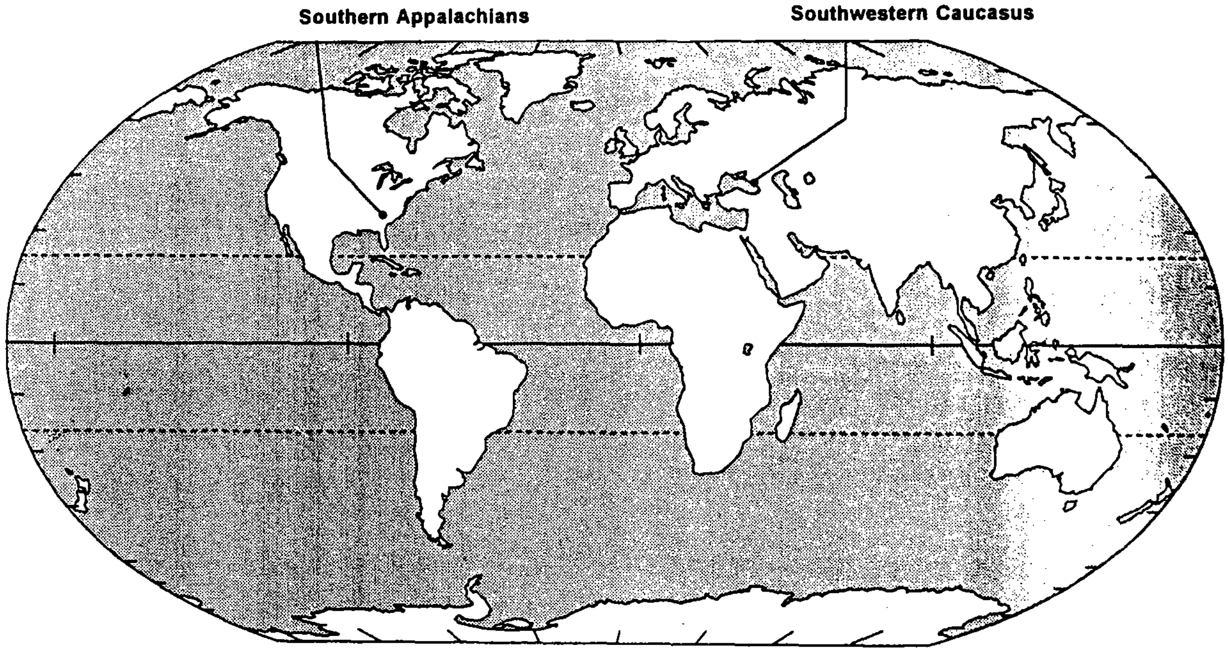

FIG. 1. Geographic location of the Southern Appalachian and Southwestern Caucasus regions of study.

Province. The coordinates of its geographical centre are approximately 35°20′ N and 83° W. The region includes the Southern Blue Ridge, Great Smoky Mountains, Balsam Mountains, Pisgah Ridge, Nantahala and Coweeta Mountains. The topography of the region is highly dissected and diverse. Widely spaced northeast–southwest oriented mountain chains are connected by numerous cross ridges (Pittillo & Smathers, 1979). The elevation ranges from about 395 m at the margin of the Piedmont to 2030 m at the summit of Mount Mitchell near the eastern border of the region, and to 2020 m at Clingman's Dome in the Great Smoky Mountains.

The warm, humid climate at the lowest elevations changes to a cool, humid climate at the mid-elevations and to a moderately cold, very humid climate at the highest elevations (Robinson, 1979) (Table 1). On the average, precipitation increases with elevation at a rate of 0.805 mm per 100 m, and the lapse rate is from 0.4°C to 0.6°C per 100 m (Whittaker, 1956; Pittillo & Smathers, 1979). The precipitation shows little seasonality except for some decreases in the late summer and autumn (Fig. 2). Snow cover is present only at the highest elevations and disappears in spring. The Southern Appalachians do not have a distinct timber line; however, some areas at the higher altitudes are occupied by subalpine-like vegetation (grassy balds).

TABLE 1. Climatic parameters for some of the Southern Appalachian and Southwestern Caucasus weather stations (Sosnin, 1939; Lasuk, 1961; *The climatic handbook of the USSR*, 1976; Pittillo & Smathers, 1979; *Climates of the States*, 1980; Swift, Cunningham & Douglas, 1987). E, altitude (m); T°C, average annual temperature; T°C min, long-term minimum temperature; $\Sigma(T°C > 0)$, sum of the mean daily positive temperatures; $\Sigma(T°C > 5)$, sum of the mean daily temperatures over five degrees; FFS, frost-free season (days); P, average annual precipitation (mm); R, average annual solar radiation (MJ/sq.m/day)

Region	Weather station	E	$T°C_{av}$	T°C min	$\Sigma(T°C>0)$	$\Sigma(T°C>5)$	FFS	P	R
Southern	Andrews	555	12.6	− 26.1	–	–	–	1568	–
Appalachians	Coweeta Main	685	12.6	− 27.8	4433	2804	180	1821	13.8
	Coweeta Mooney Gap	1365	–	–	–	–	–	2367	–
	Highlands	1015	12.1	–	–	–	–	2019	–
	Mt Mitchell	2023	6.1		–	–	–	–	–
Southwestern	Ahun	400	12.6	− 15	–	4382	240	1350	13.6
Caucasus	Krasnaia Poliana	566	9.8	− 22	3622	3414	207	1652	–
	Laura	520	8.8	− 15.4	–	–	–	2150	–
	Achishho	1880	3.7	− 28	1862	1696	131	2633	–

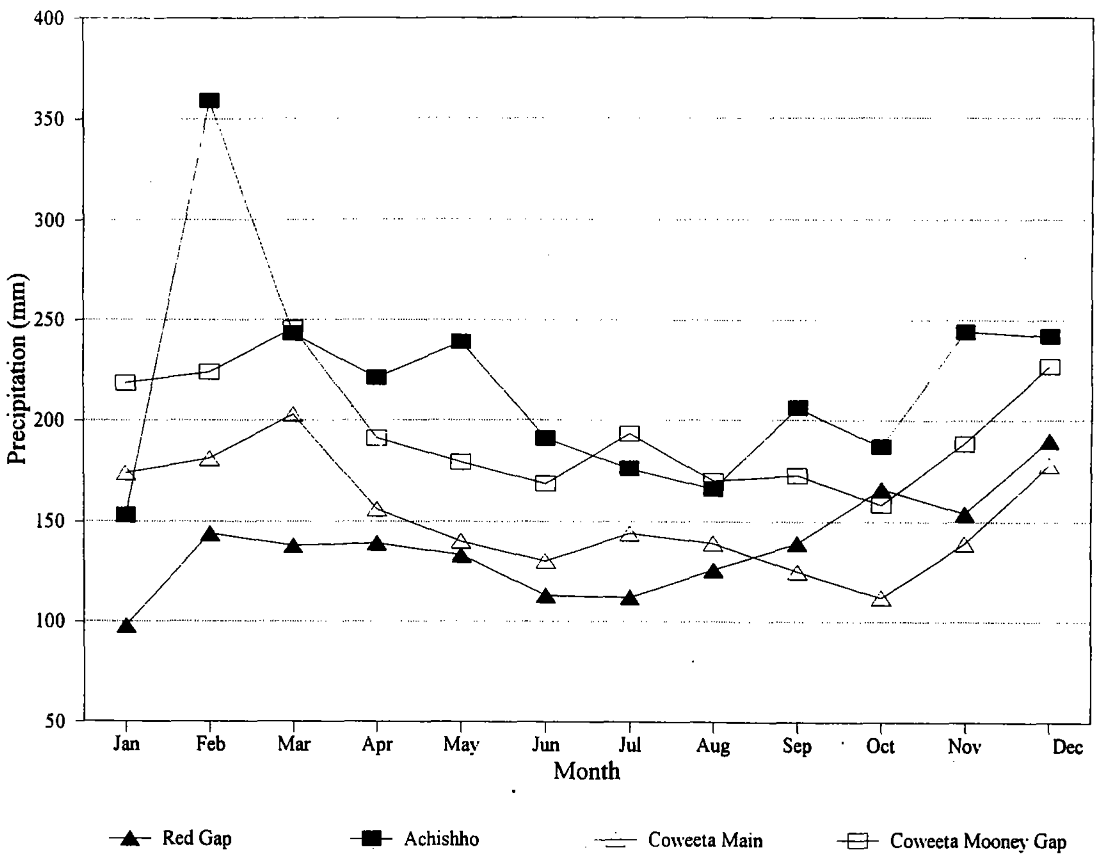

FIG. 2. Annual pattern of precipitation in the Southern Appalachians (Coweeta Main, Mooney Gap) and Southwestern Caucasus (Laura, Achishho).

Geologically the Southern Appalachian region is composed of Precambrian and, in some places, early Paleozoic crystalline rocks deposited 600–880 million years ago (Hack, 1969; Bryant & Reed, 1970; Cooper & Hardin, 1970). These rocks comprise a wide variety of granites, layered and nonlayered granitic gneiss, and migmatitic rocks (Bryant & Reed, 1970; Dietrich, 1970).

TABLE 2. Selected soil characteristics of the Coweeta basin (Southern Appalachians) and Achipse Valley (Southwestern Caucasus) (Veselov, 1973; Hutortsov, 1977; Swank & Crossley, 1988; Gorcharuk, pers. comm).

Soil characteristic	Coweeta Basin	Achipse Valley
Bulk density (gm/cub. cm)	1.24–1.52	0.73–1.68
Organic matter (%)	5.4–15.9	5–20
ph	4.74–5.13	3.5–7
Cation exchange capacity (meq 100/g)	6–11.6	3–10
Base saturation (%)	16.1–27.7	17–71
Exchangeable nutrients (mg/kg)		
K	15–22	10–20
Ca	12–71	20–40
Mg	13–20	20–40
P	1.3–6.2	<2
NH_4	3.3	3–5
Standard hydraulic conductivity of the top 0–30 cm of soil (mm/min)	10	7–11

Southern Appalachian soils were formed during a long process of erosion, which resulted in rounded and deep-soiled landscapes. The soil types are usually highly variable even at a small scale. Among the most common soil types are Hapludults and Dystrochrepts, representing two soil orders, the Ultisols and Inceptisols respectively (Table 2) (Pittillo & Smathers, 1979; Swank & Crossley, 1988).

With respect to vegetation, the Southern Appalachian region of study belongs to the Oak–Chestnut forest region (Braun, 1964) or to the Oak–Chestnut association of the mesophitic sub-Zonobiome (Greller, 1988). The major dominants of the tree layer include oak, hickory, maple, tulip poplar, and fir. The overstory composition within the area varies widely, reflecting the diversity of habitats and landforms, such as riparian zones, concave slopes ('coves'), convex slopes ('leads'), upper slopes, ridge tops, and hill 'crowns' (Whittaker, 1956; Greller, 1988).

The floristic composition of the Southern Appalachian study area was characterized using the checklists of vascular plants of the Great Smoky Mountain National Park and Coweeta Hydrologic Laboratory. Floras of the Carolinas and Southern Blue Ridge were used to increase the spatial scale of analysis.

Southwestern Caucasus

The region of study in the Southwestern Caucasus includes the western part of the southern macroslope of the main Caucasus ridge together with the Peredovoy, Prichernomorsky, and Abkhazskyi ridges. These ridges are almost parallel to the Main Caucasus Ridge and stretch from northwest to southeast. The coordinates of the geographical center of the region are 43°30′ N and 40°15′ E. Elevation varies from 200 m in the lowlands to over 3000 m on the major mountain peaks such as Chugush (3238 m) and Pseashho (3256 m).

The climate at the Southwestern Caucasus is formed under the influence of warm air transported from the Black Sea, and cyclones of the Mediterranean front. The Main Caucasus Ridge acts as a barrier that isolates the Southwestern Caucasus valleys from the influence of cool northern air masses. In general the climate is temperate and moist with mild winters (Golgofskaia, 1988) (Table 1). On average, precipitation increases by 0.747 mm and the temperature drops by 0.5°C for every 100 m of increase in altitude (Kogevnikov, 1935). The precipitation reaches its peak during the winter, whereas the driest season is the late summer (Fig. 2). The snow cover ranges from 71 cm at the average elevations up to 500 cm at the higher elevations (Romanika, 1977; Hohlov & Solodko, 1982). The snow line at the southern macroslope lies at 2730–3000 m and timber line is approximately at 2000 m.

The core of the Main Caucasus Ridge is composed of Precambrian and Paleozoic crystalline rocks, mostly granites and gneiss (Gvozdetski, 1954; Romanika, 1977). The mountains of the southern macroslope are made of Jurassic and Triassic slates, sandstones, allevrolites, argellites, massive limestone and tuffs (Romanika, 1977).

The soils of the southern macroslope of the Main Caucasus ridge belong to the Western Transcaucasian Mountain Province. Within the lower vertical zone (up to 300–500 m above sea level), either mountain zheltozems or gray forest soils predominate. Higher, up to 1800–2000 m, the soils belong to the brown mountain-forests acid non-podzolized type (Ivanova *et al.*, 1963) (Table 2). Most soils within the forest belt correspond to either Inceptisols or Ultisols in the U.S. Soil Taxonomy.

Southwestern Caucausus forests are the part of the Pontic Floristic Province (Kuznetsov, 1909). The Caucasus forest belt can be subdivided into three major elevational zones: broad-leaved forests (50–900 m), coniferous forests (900–1700 m), and high mountain krummholz forests (1700–2000 m) (Sosnin, 1939; Golgofskaia, 1988). The overstory is frequently dominated by beech, hornbeam, chestnut, oak, and fir. Micro- and mesorelief, developed by the processes of denudation and erosion across the long distinct macroslopes, play an important role in the spatial distribution of the forest communities (Golgofskaia, 1964).

Floristically, the Southwestern Caucasus study area was described using the checklists of vascular plants of the Caucasus State Biosphere Reserve and Boxwood–Yew Relict Forest. At the larger geographical scale, the flora was characterized using the checklist of vascular plants of the Abkhasian Republic (Kolakovski, 1938).

RESULTS AND DISCUSSION

Taxonomic richness

On average, the Southern Appalachian region of study has a higher taxonomic richness than the Southwestern Caucasus region (Table 3). Species richness of the forest belt in the Caucasus State Biosphere Reserve is more than 30% lower than species richness of the Great Smoky Mountains National Park, while both territories are comparable in size and elevational range (Table 3). Considerable differences also exist between the number of genera and families. The flora of the Great Smoky National Park (GRSM) is also richer than the flora of the entire Caucasus Reserve which includes the subalpine and alpine taxa. Moreover, the total number of families in the GRSM flora exceeds the number of families in the flora of Abkhasia (Table 3). This fact is quite remarkable because the Republic of Abkhasia is more than four times larger than the Great Smoky Moutains National Park and has such habitats as spacious wetlands and sea-shore lowlands, which are absent in the GRSM. At the larger spatial scale, the differences between the Southern Appalachians and Southwestern Caucasus at the family level also remain quite compelling. For example, the number of families of vascular plants in the Southern Blue Ridge Province (Southern Appalachians) is greater than the number of families in the entire Main Caucasus region (Table 3). This difference exists in spite of the fact that the Main Caucasus region has a much larger area, wider altitudinal range, and encompasses several substantially different floristic provinces such as Dagestan, Northern macroslope, etc.

Notable differences in taxonomic richness between the Southern Appalachian and Southwestern Caucasus regions can be attributed to a dramatic loss of species that occurred in the Caucasus at the end of the Tertiary period (Pliocene) (Grossgeim, 1948; Maleev, 1941). Up to that time neither region had experienced any major extinctions, and they shared the same vegetation types: paratropical forests in the Eocene, and Arctotertiary warm-temperate forests in the Miocene (Maleev, 1941; Grossgeim, 1948; Cain, 1943; Takhtajan, 1986; Tallis, 1991). The magnitude of the post-Miocene changes in the plant cover of both regions can be evaluated by comparing their contemporary and fossil Tertiary floras. According to the available paleobotanical data, at least twenty families of vascular plants from the Cretaceous and Tertiary floras of the Southeastern North America are not represented in the contemporary flora of the Carolinas (Berry, 1916, 1930; Braun, 1964; Dilcher, 1971; Radford, Ahles & Bell, 1978). In the Southwestern Caucasus the number of extinct Tertiary families is at least twenty-five (Kolakovski, 1938, 1956, 1964; Palibin, 1937; Grossgeim, 1948; Maldjavidze, 1982; Pashkov, 1965; Golgofskaia, 1988) (Appendix A). Moreover, of the forty-nine families of vascular plants in the shared Tertiary floras of the two regions, forty-four are still represented in the contemporary flora of the Carolinas, while only thirty-one are still present in the Southwestern Caucasus (Appendix B). Of the forty-four Carolina families that have survived since the Tertiary, fourteen are absent from the Caucasus, while only one Caucasus relict family is not listed in the

TABLE 3. Taxonomic richness of the Southern Appalachians and Southwestern Caucasus (Seredin, 1987; Radford *et al.*, 1978; White, 1982; Golgofskaia, 1988; Wofford, 1989). GRSM, the Great Smoky Mountains National Park; CSBR, Caucasus State Biosphere Reserve; NC + SC, North and South Carolinas; S. Blue Ridge, Southern Blue Ridge; S, species; G, genera; F, families; S/F, species-to-families ratio; S/G, species-to-genus ratio; A, area

	Appalachians			Caucasus			
	GRSM	S. Blue Ridge	NC + SC	CSBR forest belt	CSBR	Abkhasia	Main Caucasus
S	1438	2391	3360	900	1231	1994	3600
G	574	727	951	406	464	643	902
F	135	161	180	94	99	113	154
S/F	10.7	14.9	18.7	9.6	12.4	17.7	23.4
S/G	2.5	3.3	3.5	2.2	2.7	3.1	4.0
A (km^2)	2090	90,000	217,000	1880	2635	8731	162,000

contemporary flora of the Carolinas (Appendix B). All these data suggest that the flora of Southeastern North America has changed to a lesser degree than the flora of the Southwestern Caucasus, since the mid-Tertiary times.

Unlike the historic events, the present climatic and edaphic conditions of the Southern Appalachians and Southwestern Caucasus can hardly account for the observed differences in taxonomic richness. Both regions are quite similar with respect to the climatic parameters that control plant distribution in environments with ample precipitation: minimal temperatures and amount of growth-season warmth (Tivy, 1982; Larcher, 1980; Collinson, 1988) (Table 1). Additional evidence of climatic similarity is provided by the fact that such warm-temperate arborescent North American genera as *Calycantus, Carya, Clethra, Halesia, Liquidambar, Magnolia, Oxydendrum* and *Robinea* have been successfully introduced in the Southwestern Caucasus region (Golgofskaia & Kuchin, 1965; Pilipenko, 1978). Soils of the Southern Appalachians and Southwestern Caucasus overlap taxonomically and appear to have comparable ranges of parameters that can affect plant survival (Table 2) (Szafer, 1975; Tivy, 1982).

The only characteristic of the present environment that might partially account for the difference in taxonomic richness between the two regions is the geographic isolation of the Southwestern Caucasus. This region is separated from other floristic provinces by the Black Sea on the west, and by a mountain chain on the east and north. The South Appalachian region of study, on the other hand, does not have any geographic barriers which can seriously limit species migrations from adjacent floristic regions (such as Piedmont). The difference in the degree of geographic isolation explains the larger number of endemic taxa in the Southwestern Caucasus as opposed to the high percentage of exotic taxa in the Southern Appalachians (Table 4).

The question that remains to be answered in the framework of comparative analysis, is why such tree genera as *Liriodendron, Nyssa, Carya*, and many other North American and East Asian taxa which were introduced into the Southwestern Caucasus and established in a human-modified environment more than a century ago, do not naturalize in the local forests. The list of factors that may prevent this invasion includes small differences in climate and soils and competition with the native vegetation.

TABLE 4. Percentage of the relict, endemic and exotic taxa in the Great Smoky Mountains National Park (GRSM) (Cain, 1943; White, 1981) and Caucasus State Biosphere Reserve (CSBR) (Golgofskaia, 1988); Number in brackets corresponds to the percentage of the Tertiary relicts estimated using the distribution of the modern genera (Cain, 1943). No exotic taxa were reported for the Caucasus State Biosphere Reserve

	Relict taxa		Endemic taxa		
Group of plants	GRSM	CSBR	GRSM	CSBR	Exotic taxa GRSM
Tree genera	88 (93)	58	7	27	
All genera		29	12	24	
Species		17	6	16	20

TABLE 5. Plant growth forms of the Southern Appalachian and Southwestern Caucasus forests. CHL, Coweeta Hydrologic Laboratory; BYRF, Boxwood–Yew Relict Forest (Caucasus). Numbers in brackets correspond to the native taxa (Alper, 1960; Radford *et al.*, 1978; White, 1982; Golgofskaia, 1988)

Growth form	GRSM	%	CHL	%	CSBR forest belt	%	BYRF	%
Trees	126 (96)	8.8 (8.3)	61	10.1	42	4.7	30	14.5
Shrubs	136 (107)	9.5 (9.3)	59	9.8	115	12.8	33	15.9
Subshrubs	6 (5)	0.4 (0.5)	2	0.3	2	0.2	–	–
Vines	30 (22)	2.1 (1.9)	10	1.7	6	0.6	9	4.4
Herbs	1140 (920)	79.2 (80)	472	78.1	735	81.7	135	65.2

Percentage of trees and vines

The percentage of trees and vines in the floras of the Great Smoky Mountains National Park and Coweeta Hydrologic Laboratory is more than two times greater than in the Caucasus Biosphere Reserve (Table 5). This dissimilarity supports the hypothesis that these two groups of plants are among the most susceptible to climate fluctuations (Grubb, 1987). The families of arborescent plants which disappeared from the Caucasus at the end of the Tertiary period, but are represented in the Appalachians, include *Annonaceae, Hammamelidaceae, Lauraceae, Magnoliaceae, Nyssaceae, Platanaceae, Styraceae, Symplocaceae* and *Theaceae* (Kolakovski, 1938, 1956, 1964; Palibin, 1937; Grossgeim, 1948; Maldjavidze, 1982; Pashkov, 1965; Radford *et al.* 1978). The hypothesis about historical origin of the differences in the percentage of trees and vines is in part supported by the composition of the Caucasus Boxwood–Yew Relict Forest with the high percentage of the corresponding growth forms (Table 5). This forest (300 ha), protected by the moderate climate along the Black Sea shore (Ahun weather station), is assumed to have remained relatively unchanged since the mid-Tertiary (approximately 30 million years ago) (Solodko & Trostianova, 1985).

Plant families and genera

Ninety-four out of ninety-nine families of vascular plants in the Caucasus Biosphere Reserve are represented in the checklist of the Great Smoky Mountains National Park, and 112 out of 113 Abkhasian families (the exception is *Datiscaceae*) are represented in the flora of the Carolinas (Kolakovski, 1938; Radford *et al.*, 1978; White, 1982; Golgofskaia, 1988). At the level of genera, thirty-three out of thirty-four trees of the Southwestern Caucasus region are present in the flora of the Southern Appalachians (Kolakovski, 1938; Radford *et al.*, 1978). Thus, the Southwestern Caucasus flora can be seen as a nearly perfect subset of the Southeastern North American flora at the corresponding taxonomic level. This type of relationship between the two floras is the result of their similar historical origin and subsequent extinctions from the Caucasus region.

Species-to-families and species-to-genus ratios

The species-to-genus and species-to-family ratios in the Southern Appalachians and Southwestern Caucasus are quite similar (Table 3). This similarity corresponds to the assumption that the greater the number of families and genera compared to the number of species, the older the particular flora (Szafer, 1975). The flora of the Main Caucasus region (located to the north-east from the Southwestern Caucasus region) has been impacted by the Pliocene and Pleistocene climatic change, including glaciation, to a much greater degree than the flora of the Southwestern Caucasus (Gvozdetski, 1954; Tallis, 1991). The extinction of several families and genera from the Main Caucasus and more active speciation within the remaining taxonomic groups have contributed to the increasing of species-to-genus and species-to-families ratios (Table 3).

Habitat preferences of the corresponding monodominant forest communities and the sequences of overstory and understory dominants

Several monodominant forest community types are present in both the Southern Appalachians and the Southwestern Caucasus regions (Table 6). According to the available field observations, the prevalent habitat requirements for these community types are comparable. This comparability suggests that the same tree genera tend to become dominants under similar environmental conditions, in spite of the differences in historical migration patterns and contemporary levels of species richness. At the same time, the frequency of occurrence and altitudinal range of the corresponding monodominant community types can be highly variable. For example, pure beech stands in the Southern Appalachians are uncommon and are restricted to the higher elevations, while in the Caucasus beech-dominated communities are the most frequent type and occur throughout the elevational range. On the other hand, pine-dominated stands, which are quite common in the Southern Appalachians, are rare in the Southwestern Caucasus and can be found only at the higher elevations in such extreme

TABLE 6. Altitudinal ranges and habitat types of the monodominant forest community types in the Southern Appalachians and Southwestern Caucasus. Numbers indicate the average altitudinal range of occurrence (m). In the Caucasus altitudinal range was estimated only for the continental forests with the lowest elevation–400 m above the sea level (Sosnin, 1939; Whittaker, 1956; Pittillo & Smathers, 1979; Cooper, 1979).

Monodominant community type	Southern Appalachians	Southwestern Caucasus
Oak	395–1600 submesic, subxeric and xeric	400–1600 submesic and subxeric
Pine	395–1400 xeric	1700–2000 xeric
Spruce	1400–1700 mesic	1200–1800 mesic
Fir	1700–2000 mesic	1200–1800 mesic
Beech	1400–1700 mesic, submesic	400–2000 mesic, submesic

habitats as rock outcrops (Sosnin, 1939). The factors that may lead to these differences include variations in the local climate, disturbance regime, including human impacts, competition and genetic structure of the corresponding tree populations. These require further detailed investigation.

A prominent feature of the corresponding Southern Appalachian and Southwestern Caucasus forest communities is the presence of similar association sequences between the overstory and understory dominants. For example, in both regions fir forms recognizable associations with *Oxalis acetosella* L., *Dryopteris carthusiana* (Villars) H. P. Fuchs, *Vaccinium* (*V. erythrocarpum* Michx. in the Appalachians and *V. arctostaphylos* L. in the Caucausus) and *Sorbus* (*S. americana* Marsh. in the Appalachians and *S. caucasica* Zincerl. in the Caucasus) (Sosnin, 1939; Whitaker, 1956). In oak forests *Cornus* dominates understory at more xeric sites (*C. florida* L. in the Appalachians and *C. mas* L. in the Caucasus) and *Rhododendron* at more mesic sites (*R. maximum* L. in the Appalachians and *R. luteum* Sweet. in the Caucasus) (Sosnin, 1939; Mowbray & Oosting, 1968; DuMond, 1970; Racine & Hardin, 1975). The presence of analogous plant associations in both regions can be attributed to the similar environmental requirements of congeneric understory species.

CONCLUSIONS

The majority of the described similarities and differences between the Southern Appalachian and Southwestern Caucasus flora and vegetation can be attributed to the Tertiary and post-Tertiary history of both regions. These include:

differences in taxonomic richness;
differences in the percentage of tree and vine taxa;
similarities of the species-to-genus and species-to-family ratios;
similarities in floristic composition.

Differences in taxonomic richness can be at least in part attributed to the contemporary geographic isolation of the Southwestern Caucasus region. This isolation also led to the differences in the percentage of endemics between the two regions. The similarities in the habitat requirements of the monodominant forest communities and the presence of the same pairs of overstory and understory dominants can be explained by the similar edaphic and climatic conditions in both regions as well as by the comparable ecological tolerances of the congeneric species.

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APPENDIX A

The list of Tertiary families of the Eastern North America and Western Caucasus which are not represented in the contemporary floras of the Carolinas and Southwestern Caucasus.

Eastern North America

Ferns
Salviniaceae

Conifers
Cycadaceae
Taxinaceae
Podocarpaceae

Dicots
Bombacaceae
Burseraceae
Combreatceae
Dilleniaceae
Flacourtiaceae
Humiriaceae
Hydrocaryaceae
Icacinaceae
Malpighiaceae
Mimisaceae
Miristicaceae
Myrsinaceae
Ochnaceae
Papilionaceae
Proteaceae
Rhizophoraceae

Western Caucasus

Ferns
Blechnaceae

Conifers
Podocarpaceae
Taxodiaceae

Monocots
Arecaceae

Dicots
Actinidaceae
Annonaceae
Combreatceae
Eucommiaceae
Hamamelidaceae
Magnoliaceae
Meliaceae
Menispermaceae
Myricaceae
Myrsinaceae
Nyctaginaceae
Nyssaceae
Papilionaceae
Pittosporaceae
Sapindaceae
Sapotaceae
Selaginellaceae
Streculiaceae
Styracaceae
Symplocaceae
Theaceae

APPENDIX B

Families of the vascular plants that were present both in the Eastern North America and the Caucasus during the Tertiary period

A, Families represented in the contemporary flora of the Carolinas (Radford *et al.*, 1978), C, families represented in the contemporary flora of the Southwestern Caucasus (Kolakovski, 1938, Golgofskaia, 1988); (+), families represented by the exotic plants.

Family	A	C
Ferns		
Polypodiaceae	+	+
Salviniaceae		+
Conifers		
Cupressaceae	+	+
Pinaceae	+	+
Podocarpaceae		
Taxodiaceae	+	
Monocots		
Arecaceae	+	
Cyperaceae	+	+
Liliaceae	+	+
Poaceae	+	+
Potamogetonaceae	+	+
Dicots		
Aceraceae	+	+
Anacardiaceae	+	+
Annonaceae	+	
Aquifoliaceae	+	+
Araliaceae	+	+
Aristolochiaceae	+	+
Asclepidaceae	+	+
Celastraceae	+	+
Ceratophyllaceae	+	+
Combreatceae		
Ebenaceae	+	+
Euphorbiaceae	+	+
Fabaceae	+	+
Fagaceae	+	+
Guttiferae	+	+
Hamamelidaceae	+	
Juglandaceae	+	+
Lauraceae	+	+
Magnoliaceae	+	
Meliaceae	(+)	
Menispermaceae	+	
Moraceae	+	+
Myricaceae	+	
Myrsinaceae		
Nyctaginaceae	+	
Nyssaceae	+	
Oleaceae	+	+
Papilionaceae		
Platanaceae	+	+
Rhamnaceae	+	+
Rosaceae	+	+
Sapindaceae	(+)	
Sapotaceae	+	
Streculiaceae	(+)	
Theaceae	+	
Tiliaceae	+	+
Ulmaceae	+	+
Vitaceae	+	+
Total	44	31