

A new classification of the tribe Veroniceae—problems and a possible solution

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Based on the most recent evidence from phylogenetic analyses of *Veronica* and its related genera, we propose a new infratribal and infrageneric rearrangement for *Veroniceae* and *Veronica*. These recent analyses have settled the long dispute about the relationship of the Northern Hemisphere *Veronica* and the Southern Hemisphere *Hebe* complex and have shown the derivation of the latter from within the former. Other currently recognized genera such as *Synthyris* and *Pseudolysimachion* are also derived from within *Veronica*. A classification based on monophyletic genera therefore needs to either lump some well recognized genera into a large genus *Veronica* or split *Veronica* into several genera that seem impossible to separate using morphological or structural characters. We discuss the advantages and disadvantages and conclude that it is best to recognize a large genus *Veronica* (including *Hebe*, *Parahebe*, *Chionohebe*, *Heliohebe*, *Detzneria*, *Derwentia*, *Pseudolysimachion*, *Synthyris* and *Besseya*) with 13 subgenera, along with 8 other genera, *Scrofella*, *Veronicastrum* (inclusive of *Calorhabdos* and *Botryopleuron*), *Lagotis*, *Wulfenia*, *Kashmiria*, *Picrorhiza*, *Wulfeniopsis* and *Paederota*, in *Veroniceae*.

KEYWORDS: classification, *Plantaginaceae*, *Scrophulariaceae*, taxonomy, *Veronica* s.l., *Veroniceae*.

Last glacial vegetation of northern Eurasia

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Abstract

In order to investigate the potential role of vegetation changes in megafaunal extinctions during the later part of the last glacial stage and early Holocene (42e10 ka BP), the palaeovegetation of northern Eurasia and Alaska was simulated using the LPJ-GUESS dynamic vegetation model. Palaeoclimatic driving data were derived from simulations made for 22 time slices using the Hadley Centre Unified Model. Modelled annual net primary productivity (aNPP) of a series of plant functional types (PFTs) is mapped for selected time slices and summarised for major geographical regions for all time slices. Strong canonical correlations are demonstrated between model outputs and pollen data compiled for the same period and region. Simulated aNPP values, especially for tree PFTs and for a mesophilous herb PFT, provide evidence of the structure and productivity of last glacial vegetation. The mesophilous herb PFT aNPP is higher in many areas during the glacial than at present or during the early Holocene. Glacial stage vegetation, whilst open and largely treeless in much of Europe, thus had a higher capacity to support large vertebrate herbivore populations than did early Holocene vegetation. A marked and rapid decrease in aNPP of mesophilous herbs began shortly after the Last Glacial Maximum, especially in western Eurasia. This is likely implicated in extinction of several large herbivorous mammals during the latter part of the glacial stage and the transition to the Holocene.

Genome Size Variation and Evolution in *Veronica*

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Background and Aims The amount of DNA per chromosome set is known to be a fairly constant characteristic of a species. Its interspecific variation is enormous, but the biological significance of this variation is little understood. Some of the characters believed to be correlated with DNA amount are alpine habitat, life history and breeding system. In the present study, the aim is to distinguish between direct causal connections and chance correlation of the amount of DNA in the genus *Veronica*.

Methods Estimates of DNA amount were analysed for 42 members of Veroniceae in connection with results from a phylogenetic analysis of plastid trnL-F DNA sequences and tested correlations using standard statistical tests, phylogenetically independent contrasts and a model-based generalized least squares method to distinguish the phylogenetic effect on the results.

Key Results There appears to be a lower upper limit for DNA amount in annuals than in perennials. Most DNA C-values in Veroniceae are below the mean DNA C-value for annuals in angiosperms as a whole. However, the longdebated correlation of low genome size with annual life history is not significant ($P = 0.12$) using either standard statistical tests or independent contrasts, but it is significant with the generalized least squares method ($P < 0.01$).

Conclusions The correlation of annual life history and low genome size found in earlier studies could be due to the association of annual life history and selfing, which is significantly correlated with low genome size using any of the three tests applied. This correlation can be explained by models showing a reduction in transposable elements in selfers. A significant correlation of higher genome sizes with alpine habitats was also detected.

Key words: Annual life history, DNA content, genome size, independent contrasts, nucleotype, selfing, trnL-F region, *Veronica*, Veroniceae.

Fluctuating resources in plant communities: a general theory of invasibility

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Summary

1 The invasion of habitats by non-native plant and animal species is a global phenomenon with potentially grave consequences for ecological, economic, and social systems. Unfortunately, to date, the study of invasions has been primarily anecdotal and resistant to generalization.

2 Here, we use insights from experiments and from long-term monitoring studies of vegetation to propose a new theory in which fluctuation in resource availability is identified as the key factor controlling invasibility, the susceptibility of an environment to invasion by non-resident species. The theory is mechanistic and quantitative in nature leading to a variety of testable predictions.

3 We conclude that the elusive nature of the invasion process arises from the fact that it depends upon conditions of resource enrichment or release that have a variety of causes but which occur only intermittently and, to result in invasion, must coincide with availability of invading propagules.

Key-words: plant invasions, invasibility, resource availability, fluctuating resources, disturbance, exotic species

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**ESTABLISHING THE PHYLOGENETIC ORIGIN,
HISTORY, AND AGE OF THE NARROW ENDEMIC
VIOLA GUADALUPENSIS (VIOLACEAE)¹**

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- *Premise of the study:* Climate change and shifts in land use are two major threats to biodiversity and are likely to disproportionately impact narrow endemics. Understanding their origins and the extent of their genetic diversity will enable land managers to better conserve these unique, highly localized gene pools. *Viola guadalupensis* is a narrow endemic of the Guadalupe Mountains (west Texas, USA). Its affinities within *Viola* section *Chamaemelanium* have been the subject of some debate. Furthermore, the polyploid and presumably reticulate relationships within this section remain largely unknown.
- *Methods:* We counted chromosomes for *V. guadalupensis*. Phylogenies for the chloroplast *trnL-F* region and the low-copy nuclear gene *GPI* for 24 *Viola* taxa were generated and used to produce a polyploid phylogenetic network. Divergence dates were obtained by fossil calibration.
- *Key results:* Meiotic chromosome counts revealed that *V. guadalupensis* is tetraploid ($n = 12$), and the presence of two *GPI* homoeologs further suggested allotetraploidy. Phylogenetic reconstructions showed that it originated through hybridization between unidentified members of subsection *Canadenses* (paternal parent) and subsection *Nuttallianae* (maternal parent). A fossil-calibrated relaxed clock dating analysis of *GPI* estimated the maximum age of *V. guadalupensis* to be 8.6 (5.7–11.6) Myr, suggesting the species evolved after the Guadalupe Mountains formed 12–13 Ma.
- *Conclusions:* *Viola guadalupensis* originated by intersubsectional hybridization followed by polyploidization. Within section *Chamaemelanium*, this phenomenon has occurred repeatedly in the last 9 Myr (at least for *V. bakeri*, *V. douglasii*, *V. glabella*, and *V. sempervirens*). Consequences for the systematics of the section are discussed.

Key words: allopolyploid; BEAST; endemic; fossil calibration; low-copy nuclear gene; PADRE; polyploid network; *Viola guadalupensis*; Violaceae.

Dispersal limitation is stronger in communities of microorganisms than macroorganisms across Central European cities

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ABSTRACT

Aim It is generally believed that communities of small organisms, or those with small propagules, are structured mainly by local niche-based processes, and less by dispersal limitation. Conversely, weaker environmental and stronger spatial structure, indicating dispersal limitation, are expected to occur more frequently in communities of large organisms. However, this hypothesis has rarely been tested by comparing spatial and environmental effects across groups of organisms of different size (or with different size of propagules) sampled at the same set of sites. Here, we test it in urban environments.

Location Thirty-two cities in 10 countries of Central Europe and Benelux.

Methods We compared effects of spatial location and climate on species composition of different groups of organisms sampled in corresponding types of urban habitats. The studied groups were: (1) subaerial cyanobacteria and algae, (2) vascular plants, (3) land snails; and subgroups of vascular plants with different life form and dispersal mode, namely: (4) herbs, (5) animal-dispersed trees and shrubs, and (6) wind-dispersed trees and shrubs. Data were analysed by variation partitioning based on redundancy analysis (RDA) with principal coordinates of neighbour matrices (PCNM). Eighteen PCNM eigenvectors (expressing spatial effects) and mean annual temperature, July–January temperature difference and annual precipitation sum (expressing environmental effects) were used as explanatory variables.

Results Pure effects of climate on species composition, indicating niche-based processes, were not significant for any group or subgroup of the studied organisms. In contrast, pure effects of space, indicating dispersal limitation, were significant for all groups and subgroups except herbs. Surprisingly, the community of cyanobacteria/algae possessed much stronger spatial structure independent of climate than communities of larger organisms, although cyanobacteria/algae had the lowest beta diversity among the studied cities. Main conclusions We hypothesize that the community of subaerial cyanobacteria/algae is structured by natural processes which involve dispersal limitation, whereas communities of urban plants and snails are influenced by human-assisted dispersal of their propagules between cities, which results in weaker dispersal limitation. Our study indicates that dispersal vectors can be more important for community structure than size of organisms or of their propagules.

Keywords

Algae, body size, community structure, cyanobacteria, environmental filtering, land snails, spatial structure, urban ecology, variation partitioning, vascular plants.