The concept of vegetation class and order in phytosociological syntaxonomy

Javier Loidi

1 Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), Bilbao, Spain

Corresponding author: Javier Loidi (javier.loidi@ehu.eus)

Abstract

In order to stabilize the defining concepts of the higher rank syntaxonomic units such as class or order, the criteria of floristic content and unity of origin are enunciated. This is done with the aim of preventing the fragmentation of the large classes and the subsequent typological inflation. For orders, the criterion of specific floristic content is discussed, with orders that have been described to encompass seral secondary forests or the separation of forest vegetation from that which is dominated by shrubs rejected, due to their weak floristic characterization. These criteria have been applied to two forest vegetation classes: the European temperate (Querco-Fagetea) and the Mediterranean (Quercetea ilicis).

For the first, it is argued in favor of maintaining a single class for all temperate deciduous forests in Europe instead of dividing them into four. Within this single class five orders are distinguished: Fagetalia, Quercetalia roboris, Quercetalia pubescenti-petraeae, Alno-Fraxinetalia and Populetalia albae, rejecting the orders that have been proposed for secondary forests because they have few characteristic taxa. For the sclerophyllous and macchia forests of Mediterranean Europe, the Quercetea ilicis class can be split into two or three geographical orders, rejecting the Pistacio-Rhamnetalia alaterni as a shrubby physiognomic unit.

Taxonomic reference: Castroviejo S (coord. gen.) (1986–2012) Flora iberica 1–8, 10–15, 17–18, 21. Real Jardín Botánico, CSIC, Madrid, ES.

Syntaxonomic reference: Mucina et al. (2016).

Keywords

Floristic content, Quercetea ilicis, Querco-Fagetea, syntaxonomy, unity of origin, vegetation class, vegetation order

Introduction

The concept of vegetation class needs to be formalized in such a way that instability is prevented. The higher rank syntaxonomic units, such as classes, as far as they represent the fundamental parts of the ecological and floristic variability in a given territory, should have a well-defined ecology and a sufficient biological content (Pignatti et al. 1995). In terms of phytosociological syntaxonomy, each class should have a certain number of characteristic taxa; a minimal “floristic content”. As syntaxonomy reflects the floristic and ecologic relationships between the subordinate units, the higher rank units should include a significant content of a specific flora. This is particularly important in the case of classes, but it is also valid for orders. The number of taxa required to fulfill these minimal requirements are variable and must be estimated in the context of the vegetation types involved. Species rich vegetation, such as the Querco-Fagetea or Molinio-Arrhenatheretea, would need a longer list of characteristic taxa to justify the classes and orders, while species poor vegetation, such as the Calluno-Ulicetea or Cytisetea scopario-striati, have fewer taxa available for this purpose and it is usually difficult to distinguish more than one or two orders within a class in such cases.
The syntactonomic scheme structuring a class is the expression of the ecological and dynamic diversity occurring within it, but, to a certain extent, it can also express a certain biogeographical-evolutionary background. The floristic set characterizing a class has potentially originated in a particular evolutionary episode that occurred in a particular geographical area under specific environmental conditions. We could hypothesize a type of “unity of origin” in the floristic element characteristic of the class. This eco-evolutionary background should prevent us from making arbitrary decisions which are not based on real patterns in nature.

I will illustrate these ideas with a short discussion on the classes Querco-Fagetea and Quercetea ilicis.

The class Querco-Fagetea

The recent publication of the EuroVeg checklist (Mucina et al. 2016) has revived the question of the syntactonomic structuring of temperate deciduous forests in Europe. Contrary to the concept of a broad class Querco-Fagetea sylvatica, maintained by several European phytosociologists (Mucina et al. 1993, Stortelder et al. 1999), Mucina et al. (2016) decided to accept the division of this syntaxon into four European forest classes: Quercetea robori-petraeae, Carpinno-Fagetea sylvatica, Quercetea pubescentis and Alno glutinosae-Populetea albae. A different approach was presented by Rivas-Martínez et al. (2011), who proposed one class for non-riparian forests and another one for riparian forests. Other approaches have included all the fen alder and riparian ash forests in a specific class, the Alnetea glutinosae (Berg et al. 2004). A solution to this controversy requires the application of clear and objective criteria. Here, I advocate the recognition of a single class that includes most of the deciduous forests of Europe. This is supported by three broad arguments that are discussed:

1. Biogeographical-evolutionary criterion: common origin and evolution. The current European deciduous forests descend from the deciduous forests that occupied a wide area in the extratropical latitudes of the Northern Hemisphere in the first half of the Tertiary. They encompassed the territories of ancient North America and those of Eurasia. In that time they were connected by the proximity of the land masses that formed Laurasia (Axelrod 1983). The separation of North America and Eurasia and the subsequent climatic changes that occurred in the late Tertiary, gave rise to the fragmentation of that continuous zone into the three current ones: (i) North America (basically the eastern half of the USA and the southeast of Canada), (ii) Europe (to which are added areas of western Asia bordering the Black and Caspian seas), and (iii) East Asia (Sino-Japanese region comprising northeast China, the Korean peninsula, the south of the Russian Far East and the Japanese archipelago). This general context shows that the European temperate deciduous forests have a common origin followed by a common evolutionary history up to the present. Since the phytosociological class is the highest unit of the system, this unity of origin should be reflected in a single class Querco-Fagetea sylvatica. The diversity existing within it can be represented by lower syntactonomic ranks, such as the order and the alliance.

2. Floristic criterion: common set of characteristic species. After being isolated from the American and East Asian deciduous forests, the European ones shared the climatic oscillations of the Pleistocene. It is generally assumed, since Gray (1878) and Reid (1935), that the European forest flora was impoverished as a result of the extinctions that occurred during the Pleistocene glaciations, whose effects were intensified by the east-west disposition of the mountain ranges. Later it was postulated that these extinctions must have been more severe in the siliceous flora than in the basophilous one, because the siliceous territories, located mainly in the north and in the center of Europe, suffered more from the climatic rigors of the glaciations than those in the south of the continent where base-rich rocks are more abundant, allowing the basophilous flora to find more refuge areas and suffer fewer extinctions (Chytrý et al. 2003). In spite of these differences, there is a set of specific forest plants occurring throughout the European temperate deciduous forests, regardless of the substrates on which they are found, from northwestern Iberia to the Hyrcanian region south of the Caspian sea. No less than 25 forest species, from herbs such as Athyrium filix-femina, Stellaria holostea, Poa nemoralis or Brachypodium sylvaticum, to shrubs such as Rubus caesius, Daphne laureola or Frangula alnus and trees such as Acer campestre, Fraxinus excelsior, Quercus robur, Taxus baccata or Ulmus glabra, are common to most regions where these forests exist.

3. Application criterion: coherence in the presentation. Syntaxonomy has to be presented to non-phytosociologists in a useful and coherent way. It is very difficult to argue, in a teaching context, that forests dominated by the same species belong to different classes. This is also valid in other fields such as conservation, vegetation mapping or land management and planning. If we recognize four separate classes, there would be forests of Fagus sylvatica and Quercus petraea or Q. robur that would be classified into different classes. This would be unusual compared to other phytosociological syntaxonomy and further explanation would be required for students, land managers and other stakeholders, adding inconsistency and discrediting the system.

Riparian and fen forests

Riparian forests are different in several aspects from most other deciduous forests. There are three main eco-topographical positions within them: the lower bed, usually occupied by willow scrub, the upper bed, normally populated by alder and poplar forests, and the floodplain, usually dominated by ashes and elms. The forests belonging to the second and third level can be included in the class Querco-Fagetea sylvatica because they share a high number of species with the non-hygrophilous deciduous forests. However, due to their floristic and ecological spec-
 secondary forests

Several proposals to classify secondary forests have been published. Willner et al. (2016) described the order Lonicer pericyclentus-Betuletalia pubescentis, which partially corresponds to the previously described Betulo pendulae-Populetalia tremulae (Rivas-Martinez et al. 2002). Both descriptions encompass secondary forests which have become established after a certain level of disturbance. Both are also very poorly defined floristically, with the Betulo pendulae-Populetalia tremulae including a few tree species of the genus Betula, Populus tremula or Corylus avellana.

The rest of the flora is unspecific to secondary forests and occurs in many other units of the European deciduous forest, or even in forest mantles or shrublands. The floristic definition of these orders is significantly poorer than that of the other orders such as the Fagetalia sylvaticae, Quercetalia pubescenti-petraeae, Quercetalia roboris or Alno-Fraxinetalia excelsior. These orders have a clear ecological character and they have been long recognized. Secondary forests are short-lived, filling a short time window in the succession and therefore can hardly develop a specific understory flora. Before humans started transforming the landscape at the beginning of the Neolithic age, the forests of temperate Europe were overwhelmingly primary; the secondary forests only occurred after natural disturbance episodes, which were much less frequent and less extensive than after the spread of agriculture and domesticated cattle herds. Thus, they temporarily occupied naturally disturbed patches cleared by wildfire, animal herbivory, windfalls, tree disease, etc. As their floristic differentiation is weak, it would be more consistent to frame these secondary forests in associations and alliances, rather than in one or two orders.

For the reasons stated, I believe that maintaining the unity of deciduous forests in the rank of a class would be a reflection of their unity of origin and their physiognomic and ecological similarity. This argument is also supported by a significant set of species that inhabit all of them. Additionally, secondary forests do not deserve the order status due to their weak floristic characterization. I propose that within the Querco-Fagetea class there are five European orders: Fagetalia sylvaticae, Quercetalia roboris, Quercetalia pubescenti-petraeae, Alno-Fraxinetalia excelsior and Populetalia albae.

The class Quercetea ilicis

This class encompasses the sclerophyllous arboreal and shrubby vegetation in the Mediterranean region of Europe, the Middle East, and north Africa. It is a relatively species-poor unit with few herbaceous elements, due to summer drought stress and persistent shading of the understory. Distinguishing the different orders within this class has always been controversial, particularly in the western Mediterranean portion. Many of the genuine species of this class have a wide distribution across the whole Mediterranean region. In the central and eastern portion of the Mediterranean two orders have been recognized: Quercetalia calliprini and Pinetales halepensis and for the central-western area the Quercetalia ilicis has been described. Rivas-Martinez (1975) described the order Pistacia lentisci-Rhamnetalia alaterni with representation throughout the Mediterranean. This order includes the sclerophyle macchia vegetation which can act as a mantle for the arboreal communities, i.e. their first seral stage, as well as potential vegetation in the areas where climatic or edapho-topographic conditions impede the establishment of a true forest. In Mucina et al. (2016) the Quercus-dominated forest communities remained in the order Quercetalia ilicis or the Quercetalia calliprini. However, it should be
noted that some specialists in Mediterranean vegetation have published opposing views (Bolós and Vigo 1984). The characteristic species listed by Rivas-Martínez (1975) frequently occur in forests: *Asparagus hortensis*, *Chamaerops humilis*, *Clematis cirrhosa*, *C. flammula*, *Daphne gnidium*, *Euphorbia characias*, *Jasminum bruticus*, *Myrtus communis*, *Osyris alba*, *O. lanceolata*, *Pistacia lentiscus*, *P. terebinthus*, *Rhamnus alaternus*, *R. lycioides*, but the order *Pistacio-Rhamnetalia* was described based on physiognomical criterion more than floristic citerion. In our opinion, it is more sustainable and consistent to separate the *Quercetalia ilicis* into geographic orders, with the orders supported by the different endemic species which provide a firm floristic basis and confer stability to the syntaxonomy.

The relationship between the *Pistacio-Rhamnetalia* and *Quercetalia ilicis* seems to parallel that of the order *Prunetalia spinosae* and the rest of the *Querco-Fagetea*. When the order *Pistacio-Rhamnetalia* was described (Rivas-Martínez 1975), the *Prunetalia spinosae* was still accepted as an order of the *Querco-Fagetea* by most European phytosociologists, following the original concept of Tüxen (1952). The argument for establishing the *Pistacio-Rhamnetalia* was a physiognomic one (shrublands versus forests), following the criterion accepted at that time for the *Prunetalia spinosae*. However, more generally the recent opinion regarding temperate forests and forest mantles has changed, and most authors have started to accept a separate class for the spiny hedges: *Rhamno-Prunetea*, restricting the *Querco-Fagetea* to forests. At the same time, with increased knowledge of the *Quercetalia ilicis*, particularly in northern Africa (Quézel et al. 1988, 1992), a significant number of associations with a tree layer (*Pinus halepensis*, *Juniperus turbinata*, *Tétраclinis articulata*, etc.) have been described and attributed to the *Pistacio-Rhamnetalia*.

Thus, the initial separation of forests and shrubland was broken and the separation of *Pistacio-Rhamnetalia* from *Quercetalia ilicis* became inconsistent.

The *Rhamno-Prunetea* is a relatively well defined class because it has few plants in the herb layer, in strong contrast to the *Querco-Fagetea*. Concerning the shrub species, it is true that many of them are shared between both classes, particularly with the order *Quercetalia pubescenti-pe- travae*, but in the other orders, such as *Fagetalia*, most of these shrub species grow with diminished vitality. They hardly produce flowers and fruits and their populations are maintained by the constant seed rain provided by birds, as they are mostly endoozoochorous. The spiny shrubs occurring inside the forests are therefore maintained by a metapopulational dynamic as sink populations. These shrub species need high light levels to produce a good set of fruit and fertile seeds.

The *Pistacio lentisci-Rhamnetalia alaterni* is quite different from the *Prunetalia spinosae* in this respect as the shrub species exhibit good vitality within most forests. It is impossible to recognize truly characteristic shrub or tree taxa within the *Pistacio lentisci-Rhamnetalia alaterni* and the herb species are limited and generally unspecific.

**Acknowledgements**

I wish to thank Jim Martin for the linguistic editing and suggestions in the text and the comments of an anonymous reviewer that have helped me to arrive at a better version of the manuscript, but I am especially grateful to Wolfgang Willner for his in-depth review and participation in the production of a more complete and scientifically sound final version.

**References**

Axelrod DI (1983) Biogeography of oaks in the Arco-Tertiary Province. Annals of the Missouri Botanical Garden 70: 629–657. https://doi.org/10.2307/2398982

Berg C, Dengler J, Abdank A, Isserman M (2004) Die Pflanzenge- sellschaften Mecklenburg-Vorpommerns und ihre Gefärdung – Textband. Weidorn-Verlag, Jena, DE.

Buurrun I, Campos JA, Garcia-Mijangos I, Herrera M, Loidi J (2016) Floodplain forests of the Iberian Peninsula: Vegetation classification and climatic features. Applied Vegetation Science 19: 336–354. https://doi.org/10.1111/avsc.12219

Bolós O, Vigo J (1984) Flora dels Països Catalans. Vol. 1. Ed. Barcino. Barcelona, ES.

Chytrý M, Tichý L, Roleček J (2003) Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. Folia Geobotanica 38: 429–442. https://doi.org/10.1007/BF02803250

Gray A (1878) Forest geography and archaeology. American Journal of Sciences and Arts, Ser. 3, 16: 85–95, 183–196. https://doi.org/10.2475/ajs.s3-16.93.183

Mucina L, Búltmann H, Dierßen K, Theurillat J P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Mucina L, Grabherr G, Wallnöfer S (1993) Die Pflanzengesellschaften Österreichs. Teil III. Wälder und Gebüsche. Gustav Fischer, Jena, DE.

Pignatti S, Oberdorfer E, Schaminée JHJ, Westhoff V (1995) On the concept of vegetation class in phytosociology. Journal of Vegetation Science 6: 143–152. https://doi.org/10.2307/3236265

Quézel P, Barbero M, Benabid A, Loisel R, Rivas-Martínez S (1988) Contribution à l’étude des groupements pré-forestiers et des matorrals rifiannes. Ecologia Mediterranea 14: 77–122. https://doi.org/10.3406/ecmed.1988.1208

Quézel P, Barbero M, Benabid A, Rivas-Martínez S (1992) Contribution à l’étude des groupements forestiers et pré-forestiers du Maroc oriental. Studia Botanica 10: 57–90.

Reid EM (1935) Discussion on the origin and relationship of the British flora. Proceedings of the Royal Society of London, series B, Biological Sciences 118: 197–214. https://doi.org/10.1098/rspb.1935.0054

Rivas-Martínez S (1975) La vegetación de la clase Quercetea ilicis en España y Portugal. Anales del Instituto Botánico Cavanilles 31(2): 205–259.
Rivas-Martínez S, Díaz TE, Fernández-González F, Ixco J, Loidi J, Lousá M, Penas A (Eds) (2002) Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. Itinera Geobotanica 15: 5–922.

Rivas-Martínez S, Asensi A, Garretas B, Mesa J, Valle F, Cano E, Costa M, Díaz T, Fernández Prieto JA, ... Soriano P (2011) Mapa de series, geoseries y geopermaseries de vegetación de España (Memoria del mapa de vegetación potencial de España), Parte II. Itinera Geobotanica 18: 5–424.

Stortelder AHF, Schaminée JHJ, Hermy M (1999) Querco-Fagetea. In: Stortelder AHF, Schaminée JHJ, Hommel PWFM (Eds) De vegetatie van Nederland, deel 5, plantengemeenschappen van ruigten, struweel- en bossen, Opulus, Uppsala, SE, 287–331.

Tüxen R (1952) Hecken und Gebüsche. Mitteilungen der Geographischen Gesellschaft Hamburg 50: 85–117.

Willner W, Solomeshch A, Čarni A, Bergmeier E, Ermakov N, Mucina L (2016) Description and validation of some European forest syntaxa – a supplement to the EuroVegChecklist. Hacquetia 15: 15–25. https://doi.org/10.1515/hacq-2016-0005

E-mail and ORCID

Javier Loidi (Corresponding author, javier.loidi@ehu.eus), ORCID: https://orcid.org/0000-0003-3163-2409