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# Biogeography of Flowering Plants: A Case Study in Mignonettes (Resedaceae) and Sedges (*Carex*, Cyperaceae)

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## 1. Introduction

Biogeography is a multidisciplinary science that studies the past and present geographic distribution of organisms and the causes behind it. The combination of historical events and evolutionary processes has usually an outstanding role when explaining the shape of a species range. As already noted by Darwin more than 150 years ago, patterns of species distribution may often be seen as clear footsteps of their evolution and diversification (Darwin, 1859). It is now also well known that geological events (i.e. continental drift, orogeny or island formation) and climatic oscillations occurred during the recent geological history of the Earth, like the cooling and aridification that took place during the Pliocene (5.3 – 2.5 million years ago, m.a) and the Pleistocene glaciations (1.8 – 0.01 m.a), prompted great range shifts. These geological and/or climatic changes caused, in some cases, the extinction of species; in many others, they provided conditions of reproductive isolation and/or genetic divergence between populations and, eventually, produced speciation, the engine of biodiversity.

The development of molecular techniques to study biodiversity from the end of the XX<sup>th</sup> century has implied a great methodological revolution in the field of systematics, evolutionary biology and biogeography. They constitute valuable and powerful tools that allow tackling multiple biogeographic and evolutionary hypotheses, as well as to progress towards a natural classification of biodiversity that reflects its evolutionary history. In particular, these methodological advances have boosted the study of the principles and historical processes behind the geographical distribution of genetic lineages at low taxonomic levels, in the recently arisen discipline termed phylogeography (Avise et al., 1987; Avise, 2000). Phylogeography is a multidisciplinary science that integrates methods and concepts from population genetics (“microevolution”) and systematics (“macroevolution”) (Avise, 2000).

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Biogeographic studies using molecular approaches have helped to elucidate the origin of striking bipolar or intercontinental range disjunctions and to estimate the divergence time between allopatric populations or taxa (e.g. Dick et al., 2007; Donoghue, 2011; Givnish & Renner, 2004; Milne, 2006; Mummenhoff & Franzke, 2007; Popp et al., 2011; de Queiroz, 2005; Renner, 2005; Shaw et al., 2003; Wen & Ickert-Bond, 2009), the causes of disparate species or lineage richness in different territories (e.g. Ricklefs et al., 2006; Svenning et al., 2008; Valente et al., 2010, 2011), or the reconstruction of ancestral ranges (e.g. Drummond, 2008; Fernández-Mazuecos & Vargas, 2011; Mansion et al., 2009; Salvo et al., 2010). In this chapter, we briefly review the main methodological approaches that have enabled the rise of biogeographic and phylogeographic studies in plants based on molecular data during the last decade. Specifically, as a case study, we review researches that have successfully applied molecular methods to address biogeographic questions in two plant groups, a dicot (family Resedaceae) and a monocot (genus *Carex* L., Cyperaceae).

## 2. Methods in molecular biogeographic and phylogeographic studies

### 2.1 Molecular markers

One of the critical points in molecular biogeographic and phylogeographic studies of plants is the availability of DNA regions that provide an adequate level of reliable molecular variability at the studied taxonomic level (Schaal et al., 1998). Bio- and phylogeographic markers should preferentially be ordered (DNA sequences), rather than unordered (e.g. AFLP, ISSR, RAPD), thus containing a record of their own histories and providing information about genealogical relationships between alleles (e.g. Lowe et al., 2004; Schaal & Leverich, 2001; Schaal & Olsen, 2000).

Sequences from organellar genomes (mitochondrial and plastid DNA) have played a key role in phylogeographic studies. While mitochondrial DNA has been extensively used in animals, it has been scarcely used in plants (but see Sinclair et al., 1998; Tomaru et al., 1998) as this genome is usually not sufficiently variable in plants and is commonly submitted to intramolecular recombination (Palmer, 1992). Many plant phylogeographic studies have relied on the plastid genome, since is more variable than mitochondrial DNA, recombination processes are not frequent, and it is usually uniparentally inherited (maternally in most angiosperms; Harris & Ingram, 1991). It has also a reduced effective population size in comparison to the nuclear genome due to its haploid nature. This feature results in an increased effect of genetic drift reflected in a greater genetic differentiation of fragmented populations. Thus, plastid regions may longer retain phylogeographic signals of past migrations, range fragmentation and dispersal events (e.g. Hudson & Coyne, 2002; Kadereit et al., 2005; Newton et al. 1999; Petit et al., 2005; Rendell & Ennos, 2003; Schaal et al., 1998).

At the first stages of phylogeography, the most widespread technique for detecting molecular variation within plastid genome used to be restricted fragment length polymorphism (RFLPs, PCR-RFLPs; Hampe et al., 2003; Mason-Gamer et al., 1995; Wagner et al., 1987; review in Soltis et al., 1992). More recently, to avoid homoplasy problems, direct sequencing of non-coding regions of plastid genome has become prevalent (e.g. Hung et al., 2005; Jakob & Blattner., 2006; Koch et al., 2006). Nonetheless, due to its biparental inheritance, genealogical patterns inferred from nuclear markers are probably more representative of the true evolutionary history and gene flow patterns than those derived

from organellar genomes (Harpending et al., 1998; Lowe et al., 2004). Nuclear ribosomal internal transcribed spacer (ITS) sequences have been widely used in phylogenetic and biogeographic studies. Among the characteristics that explain the success of this marker are the almost universal primers and a high number of copies in the genome, which greatly eases PCR amplification. In addition, ITS usually provides an appropriate level of variability at the generic and infrageneric level (reviews in Álvarez & Wendel, 2003; Calonje et al., 2009; Nieto Feliner & Rosselló, 2007). However, the use of this marker has been also criticized due to its multicopy nature and concerted evolution processes, which frequently results in high levels of homoplasy (Álvarez & Wendel, 2003; Bailey et al., 2003). Single or low-copy nuclear genes have been also used for phylogeographic studies, although its experimental tuning is usually complex (Caicedo & Schaal, 2004; Olsen, 2002; Olsen & Schaal, 1999; reviews in Hare, 2001; Pleines et al., 2009). In addition, in this case, issues derived from the dynamics of nuclear genome, like recombination and loci homology, may complicate the analysis of its molecular variation (Hare, 2001; Schaal et al., 1998; Schierup & Hein, 2000; Zhang & Hewitt, 2003). Fingerprinting techniques, like microsatellites (SSRs; review in Ouborg et al., 1999) and AFLPs (Rubio de Casas et al., 2006; Tremetsberger et al., 2006; review in Meudt & Clarke, 2007), and, to a lesser extent, RAPDs and ISSRs (e.g. Clausen et al., 2000; Hess et al., 2000), are currently also frequently used for phylogeographic studies, due to the generally high levels of variability retrieved (review in Pleines et al., 2009). SSRs have the advantage of being a codominant marker of known genetic origin, while AFLPs, ISSRs and RAPDs are anonymous and dominant markers (e.g. Lowe et al., 2004; Mueller & Wolfenbarger, 1999). In these cases, inferences about evolutionary history of populations are not interpreted from genealogical relationships of the markers, but from patterns of genetic diversity and differentiation of populations or groups of populations. Nevertheless, studies on the evolutionary history of species or populations based on genealogical relationships retrieved from unordered markers such as AFLPs have become more common in recent years (Beardsley et al., 2003; Tremetsberger et al., 2006; Pearse & Hipp, 2009). Finally, the latest advances in sequencing techniques, such as restriction-site associated DNA (RAD) and “genotyping-by-sequencing” (GBS) markers, are already being used in biogeographic and phylogeographic studies (Baird et al., 2008; Elshire et al., 2011; review in Davey et al., 2011).

## 2.2 Reconstruction of genealogical relationships using DNA sequences

The analysis and interpretation of genealogical relationships of alleles is one of the main issues of biogeography and phylogeography. The first approaches for disentangling genealogies of alleles were based on bifurcate phylogenetic reconstruction methods using parsimony (as implemented in PAUP (Swofford, 2003) or TNT (Goloboff et al., 2008)), maximum likelihood (as implemented in PAUP (Swofford, 2003) or PAML (Yang, 1997)) and/or Bayesian (as implemented in MrBayes; Ronquist & Huelsenbeck, 2003) approaches (review in Page & Holmes, 2004). The two latter apply evolutionary models of nucleotide substitution (see Posada, 2008). In the last years, reconstruction of genealogical relationship of alleles for phylogeographic studies is usually performed from the basic conceptual framework of coalescent theory (reviews in Ewens, 1990; Fu & Li, 1999; Hudson, 1990; Tavaré, 1984). Accordingly, the coalescent theory has been also implemented in phylogenetic methods (Drummond & Rambaut, 2007; BEAST software). This theory predicts the effects of different processes (genetic drift, mutation, selection) on the evolution of

alleles. At low taxonomic levels, the frequent intervention of biological processes like reticulation and persistence of ancestral alleles may not always be accurately represented with standard, bifurcate phylogenetic trees. Therefore, allele genealogies are more appropriately represented with haplotype networks (Huson & Bryant, 2006; McBreen & Lockhart, 2006; Posada & Crandall, 2001). Haplotypes are inferred from nucleotide polymorphisms in DNA sequences. In a species, gene alleles (either sampled, unsampled or extinct) derive from a common ancestral allele in which all coalesce (Schaal & Leverich, 2001). Genealogical relationships of haplotypes may be interpreted together with the patterns of congruence between haplotype frequency and their geographical distribution. This may allow to infer historical processes in the evolutionary history of species and/or populations, like range expansion or fragmentation, geographical isolation, gene flow, genetic bottlenecks, or incomplete lineage sorting of ancestral polymorphisms (Schaal et al., 1998; Schaal & Olsen, 2000).

Reconstruction of genealogical networks, in parallel to that found for phylogenetic inference (review in Page & Holmes, 2004), may be based in distance or character methods (reviews in Huson & Bryant, 2006; McBreen & Lockhart, 2006; Morrison, 2005). Among the first stand split decomposition (Bandelt & Dress, 1992) and neighbor-net (Bryant & Moulton, 2004). On the other hand, character methods include joining networks (Median-joining network, Bandelt et al., 1999; median network, Bandelt et al., 2000) and, especially, the widely used statistical parsimony (Templeton et al., 1992), which represents each change between two haplotypes as a mutational step (Clement et al., 2000; TCS software). Networks may be also reconstructed from phylogenetic trees, such as with consensus networks (Holland et al., 2004, 2006) or super-networks (Huson et al., 2004).

Recently, species trees methods based on coalescent theory have been developed which may be useful to deal with phylogenetic incongruences between different genes or genomes, for example when processes of incomplete lineage sorting or hybridization are involved (Blair & Murphy, 2011; Degnan & Rosenberg, 2009; Liu et al., 2009; Zachos, 2009). Moreover, “isolation-with-migration” methods simultaneously model the differentiation of the species / populations and the hybridization/gene flow rates between them (Becquet & Przeworski, 2007, 2009; Hey & Nielsen, 2004, 2007; Wilkinson-Herbots, 2008). This area is currently at the fore of phylogenetics and holds considerable promise for the methodological development of the analysis and interpretation of genealogical relationships of alleles.

### **2.3 Reconstruction of genealogical relationships and genetic structure using fingerprinting data**

When analyzing fingerprinting data for the reconstruction of genealogical relationships, phylogenies based on pairwise genetic distance among individuals, populations or species are widely used. Nei & Li's (1979) and Jaccard's coefficients are by far the most commonly used to calculate pairwise genetic distances between individuals from AFLP, RAPD or ISSR data (1/0 matrices), accounting only for allele presence matches (1). In contrast, the simple matching coefficient considers both presence (1) and absence (0) matches, which is considered less accurate (see Weising et al., 2005). Other genetic distances or coefficients widely used for AFLP, RAPD or ISSR (often to calculate genetic distances between populations) are pairwise  $F_{st}$  values and Nei's distances (see Lynch & Milligan, 1994; Nei, 1978). For SSR data, DA genetic distance based on allele frequencies (Nei et al., 1983) is one



of the most widely used. The election of the measure of genetic distance depends on the organism level (individual, population or species), the analyzed marker (AFLP, RAPD, ISSR or SSR) and the particular study goals. Pairwise genetic distances are depicted by dendrograms, which may be reconstructed with different methods: UPGMA (unweighted pair-group method using arithmetic averages; Sneath & Sokal, 1973; Sokal & Michener, 1958), minimum evolution (ME, Edwards & Cavalli-Sforza, 1963; Kidd & Sgaramella-Zonta, 1971; Rzhetsky & Nei, 1993) and neighbor joining (NJ; Saitou & Nei, 1987). At present, NJ and ME, which do not assume constant evolutionary rate along all branches, are the most widely used methods. Genetic relationships among individuals are also frequently represented with the principal coordinate analysis (PCO) for 1/0 matrices and the principal component analysis (PCA) for allele frequency matrices. As already noted, inferences about evolutionary history of populations are not usually interpreted from genealogical relationships of haplotypes, but from patterns of genetic diversity or population differentiation. Some of the most widely used genetic diversity indices are percentage of polymorphic loci (P), allelic richness (A), effective number of alleles ( $A_e$ ), Shannon index and Nei's index (Lynch & Milligan, 1994; Nei, 1973). For estimation of genetic differentiation,  $F$  Statistics ( $F_{st}$ ) and related measures have been widely used (Wright, 1951; see Weising et al., 2005); however, at present, AMOVA (Excoffier et al., 1992) is considered a more accurate approach as it does not assume Hardy-Weinberg equilibrium. In the last years, Bayesian analyses for disentangling population genetic structure have been developed, as implemented in STRUCTURE (Pritchard et al., 2000) or in BAPS (Corander et al., 2003) softwares.

## 2.4 Ancestral range reconstruction

Extinction, dispersal and vicariance are important historical factors to explain a current taxon range. The combination of them has frequently caused disjunct ranges, including remarkable patterns such as bipolar, intercontinental or trans-oceanic disjunctions. The study and interpretation of disjunctions have been one of the most fascinating aspects of plant biogeography and phylogeography (e.g. Givnish & Renner, 2004; Milne, 2006; Raven, 1972; Thorne, 1972; Wood, 1972; Zhengyi, 1983). One of the most widely used methodological approach to elucidate the origin of disjunctions and patterns of colonization and dispersal has been the estimation of divergence times (see 2.5) and ancestral range reconstruction. The latter method maps extant taxa distributions on molecular phylogenies. In the last years, new algorithms have been developed to improve the reconstruction of the evolutionary history of non-molecular characters using molecular phylogenies. Three different approaches have been implemented for ancestral character mapping and biogeographical inference in phylogenetic reconstruction: (1) parsimony (DIVA software: Ronquist, 1997; Mesquite software: Maddison & Maddison, 2010; S-DIVA software: Yu et al., 2010), (2) maximum likelihood (Schluter et al., 1997; Lagrange software: Ree et al., 2005, Ree & Smith, 2008; Mesquite software: Maddison & Maddison, 2010), and (3) Bayesian (SIMMAP software: Bollback, 2006; Bayes-DIVA software: Nylander et al., 2008, Sanmartín et al., 2008). Some of these tools (e.g. DIVA, Lagrange) were specifically developed for the reconstruction of geographical areas, while others were designed for the study of morphological character evolution (e.g. Mesquite, SIMMAP). However, mapping of ancestral distributions and its implementation in software intended for morphological character mapping have been criticized, because species distributions are not expected to

follow the same models as morphological characters (Ree et al., 2005). Methods that assume dispersalist or center-of-origin mechanisms have been criticized by some authors who argue in favour of vicariance (Humphries & Parenti, 1999). Specific methods for ancestral range reconstruction and morphological character reconstruction were compared by Clark et al. (2008). They concluded that the methods which consider branch lengths (dispersal-extinction-cladogenesis and stochastic character mapping) usually yield the most plausible biogeographic hypotheses (see also Buerki et al., 2011; Ree & Sanmartín, 2009). Very recently, a new approach based on speciation, extinction and dispersal rates has been developed (geographic state speciation and extinction model, GeoSSE; Goldberg et al., 2011). It combines features of the constant-rates birth-death model with a three state Markov model. This software allows the codification of three different areas, of which two are contained in the third, a widespread one. The output parameterizes speciation, extinction and dispersal rates among the two distinct areas (Goldberg et al., 2011).

## 2.5 Estimation of divergence times

The development of methods for molecular dating is currently one of the most active fields of research within plant biogeography and phylogeography. The basis of molecular dating is that a direct relationship exists between the degree of molecular divergence between two taxa and the time elapsed since their divergence from a common ancestor. Therefore, it provides a temporal context that allows relating important processes during the evolutionary history of a taxon (speciation, extinction, radiation) with palaeogeologic/climatic events. Estimation of divergence times were, at the first stages of molecular systematics, based in proteins (Zuckerkandl & Pauling, 1962, 1965) that were progressively replaced by DNA sequences.

The molecular clock hypothesis, which assumes a relatively constant rate of molecular divergence through time, has been one of the most debated concepts of molecular biology (e.g. Hillis et al., 1996; Sanderson, 1998; Sanderson & Doyle, 2001). Many researchers soon rejected that DNA mutation rates were constant (Simpson, 1964; Mayr, 1965). Statistical approaches were subsequently developed to evaluate the constancy of the evolutionary rate among different lineages, like the relative ratio test (Sarich & Wilson, 1967) or the Langley & Fitch (1974) test. Nowadays it is well known that DNA evolves heterogeneously at different organization levels, from the nucleotide positions in a codon, to different genes or regions, genomes, and organisms (Britten, 1986; Bromham & Penny, 2003; Graur & Li, 2000; Li, 1997; Wolfe et al. 1987). Several factors may influence nucleotide mutation rate as much as or even more than chronological time, like the organism's generation time (Laird et al., 1969; Li et al., 1987; Ohta, 1995) or the metabolic rate (Martin & Palumbi, 1993).

If molecular clock hypothesis is assumed, estimation of divergence time may be calculated with the method of mean path length (Bremer & Gustafsson, 1997; Britton et al., 2002, PATH software) that applies a linear regression (Graur & Li, 2000; Nei, 1987). Constant mutation rate may be also optimized with maximum likelihood (Felsenstein, 1981; Langley & Fitch, 1974). Rejection of the constant rate hypothesis may lead to pruning tree branches that do not fit the hypothesis (linearized trees, Li & Tanimura, 1987), or applying "local" molecular clocks, which assume a relatively constant rate between related lineages (Hasegawa et al., 1989; Rambaut, 2001, maximum likelihood approach in RHINO software; Rambaut & Bromham, 1998, maximum likelihood approach in Qdate software; Yang, 1997, maximum likelihood approach in PAML/BASEML software; Yoder & Yang, 2000). More recently,

methodological advances have enabled the application of variable mutation rates, as well as to integrate palaeontological information, which allows a more realistic and accurate estimation of divergence times (reviews in Magallón, 2004; Rutschmann, 2006; Sanderson et al., 2004). Some of the most widespread methods currently used implement mutation rate “smoothing”, like the non-parametric rate smoothing (Sanderson, 1997) and the semiparametric method of penalized likelihood (Sanderson, 2002, 2003, r8s software), based on the maximum likelihood criterium. Bayesian inference approaches to molecular dating have been also developed (Aris-Brosou & Yang, 2002, PhyBayes software; Drummond & Rambaut, 2007, BEAST software; Huelsenbeck et al., 2000; Kishino et al., 2001; Thorne et al., 1998; Thorne & Kishino, 2002, Multidivtime software). The use of parametric methods for estimating divergence times is also becoming widespread, as they are believed to be more reliable than non-parametric or semiparametric approaches (Drummond & Rambaut, 2007, BEAST software; Thorne & Kishino, 2002, Multidivtime software).

When dealing with fairly recent events in the evolutionary history of organisms, molecular dating needs to be based on rapidly evolving markers such as DNA fingerprinting, due to the usual lack of nucleotide variability found among DNA sequences. Accordingly, a method for the estimation of absolute times of diversification using an AFLP clock approach has been developed (Kropf et al., 2009). They found that the degree of AFLP divergence between mountain phylogroups in different alpine species was significantly correlated with their time of divergence (as inferred from palaeoclimatic/palynological data), indicating constant AFLP divergence rates. Nevertheless, this method was criticized by Ehrich et al. (2009), because the relationship between genetic distance and time in Kropf et al.’s (2009) data was not always linear, and also due to the potential bias introduced by intrapopulation genetic diversity in the suggested genetic distance ( $D_{72}$ ; Nei, 1972).

Molecular dating analyses usually result in a chronogram, this is, a phylogenetic tree that explicitly represents chronological time with branch lengths. It is generally assumed that estimates of divergence time must be considered cautiously (e.g. Hillis et al., 1996). One of the main problems in molecular dating is calibration, which is the inclusion of independent (non-molecular) chronological information within the phylogeny, in order to transform relative to absolute time (Heads, 2005; Magallón, 2004; Reisz & Müller, 2004; Rutschmann et al., 2007). Calibration should be based preferentially in fossils, or, failing that, on palaeogeological events (i.e. continental vicariance, ages of oceanic islands or mountain ranges). However, fossils only provide a lineage’s minimum age (Benton & Ayala, 2003; Magallón, 2004). Incongruences between age estimates inferred from molecular data and fossil record have been often found (Pulquério & Nichols, 2007; Sanderson et al., 2004; Steiper & Young, 2008). Likewise, resulting age estimates may display significant differences according to sampling, methods, calibration points, or DNA region analysed (e.g. Linder et al., 2005; Magallón, 2004; Magallón & Sanderson, 2005; Sanderson et al., 2004; Sanderson & Doyle, 2001).

### 3. A case study in Resedaceae and *Carex* L. (Cyperaceae)

#### 3.1 Study groups

##### 3.1.1 Resedaceae

The Resedaceae is a small family included in order Brassicales and composed of six genera (*Caylusea* A. St. Hil, *Ochradenus* Del., *Oligomeris* Cambess., *Randonia* Coss., *Reseda* L. and



*Sesamoides* All.; Fig. 1) and ca. 85 species mainly distributed in temperate areas of the Old World (Fig. 2A), with the main centre of diversity around the Mediterranean Basin. Most species grow in sunny and arid habitats, like steppes, deserts and dry slopes, and generally prefer basic soils. In five of the six genera of the family, some (in *Caylusea* and *Reseda*) or all of their species (in *Ochradenus*, *Oligomeris* and *Randonia*) live in desert and subdesert regions. There are also some ruderal species in genus *Reseda* that occur in waste grounds and disturbed places, and a few are confined to mountainous areas. Four genera are mostly composed of annual or perennial herbs (*Caylusea*, *Oligomeris*, *Reseda* and *Sesamoides*), while the remaining two are formed of shrubs (*Ochradenus*, *Randonia*).

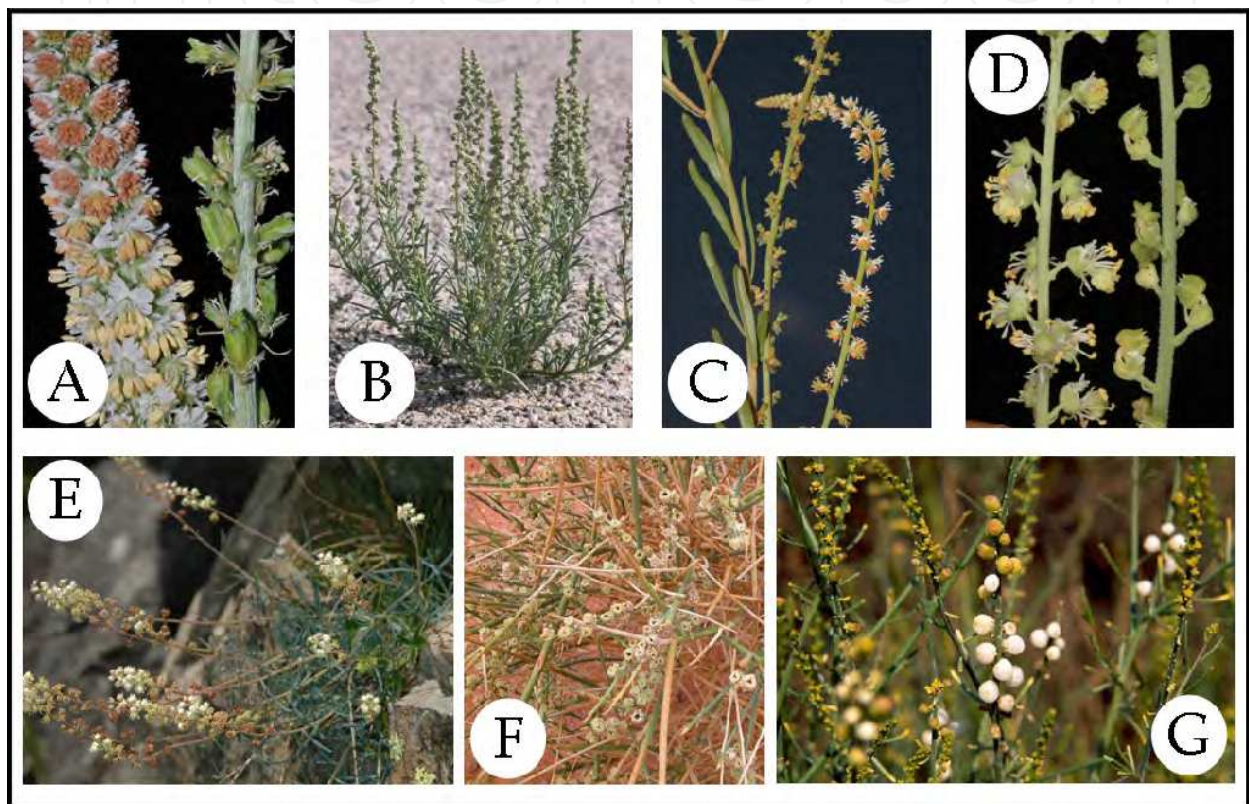


Fig. 1. Representatives of family Resedaceae: A) *Reseda barrelieri* Müll. Arg.; B) *Oligomeris linifolia* (Vahl) J.F. Macbride; C) *Sesamoides purpurascens* (L.) G. López; D) *Caylusea hexagyna* (Forssk.) M.L. Green; E) *Reseda glauca* L.; F) *Randonia africana* Coss.; G) *Ochradenus baccatus* Del.

One of the three species of *Caylusea* occurs in desert regions of the Old World, from Cape Verde archipelago across N Africa to SW Asia, while the remaining two are found in the mountains of NE Tropical Africa (Abdallah & de Wit, 1978; Taylor, 1958; Fig. 2B). *Ochradenus* (9 spp.; Abdallah & de Wit, 1978; Miller, 1984) is distributed in desert regions from Central-North Africa to SW Asia (Fig. 2C). *Oligomeris* (3 spp.; Abdallah & de Wit, 1978) displays interesting range disjunctions, with two species endemic to SW Africa and another widespread from the Canary Islands to SW Asia through N Africa, which also includes disjunct populations in SW North America (Fig. 2D). *Randonia* is a monotypic genus (Abdallah & de Wit, 1978; Miller, 1984) confined to gypsum soils of Central and Western Sahara Desert (Fig. 2E). *Reseda*, with ca. 65 species (Abdallah & de Wit, 1978; Müller

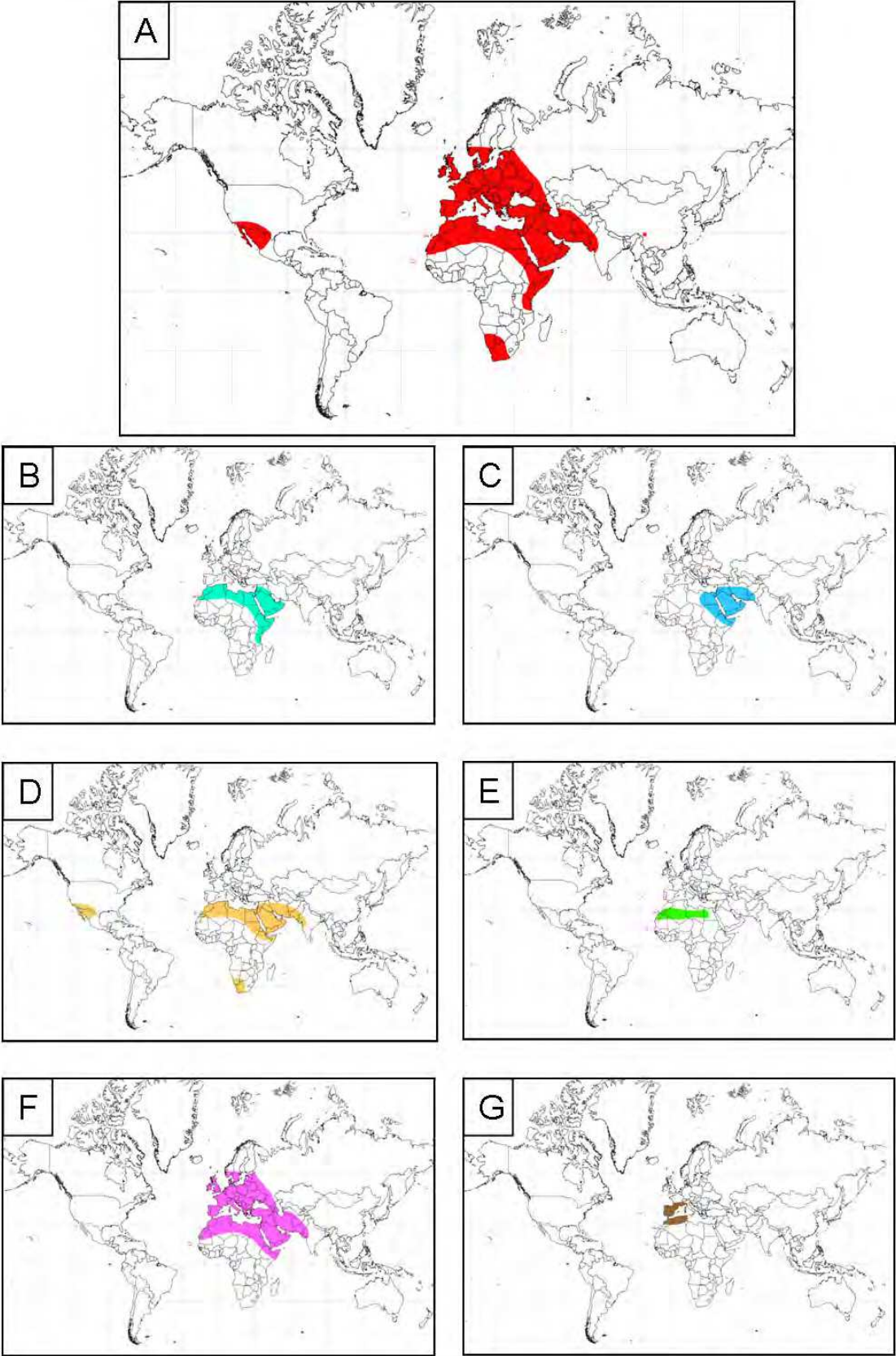


Fig. 2. Approximate distribution of A) family Resedaceae, and its genera: B) *Caylusea*; C) *Ochradenus*; D) *Oligomeris*; E) *Randonia*; F) *Reseda*; G) *Sesamoides*.



Argoviensis, 1868), is by far the largest genus of the family, and its distribution is clearly centered on the Mediterranean Basin (Fig. 2F), with two regions of high species richness, one in the Western and the other in the Eastern Mediterranean and SW Asia. A few of its species has spread as introduced weeds in many temperate regions of the world. Finally, *Sesamoides* (1-6 spp; Abdallah & de Wit, 1978; López González, 1993; Müller Argoviensis, 1868) is endemic to the Western Mediterranean region (Fig. 2G).

### 3.1.2 *Carex*

*Carex* L. (Cyperaceae) is distributed worldwide, with a diversification centre in temperate regions of the Northern Hemisphere. With ca. 2000 species, this genus probably ranks among the four most diversified of angiosperms, and is by far the largest in the temperate regions of the Northern Hemisphere (only the genera *Astragalus*, *Rosa* and *Euphorbia* may contain more species than *Carex*; Judd et al., 2007). Within genus *Carex*, we have studied two species groups. On one hand, there are six species (*C. canescens* L., *C. macloviana* D'Urv. and *C. maritima* Gunn. from subgenus *Vignea* (P. Beauv. Ex T. Lestib.) Peterm., *C. arctogena* Harry Sm. and *C. microglochin* Wahlenb. from subgenus *Psyllophora* (Degl.) Peterm., and *C. magellanica* Lam. from subgenus *Carex*; Fig. 3 A-F) which display a bipolar distribution (Fig. 4). This means that their populations occur in the high latitudes of both the Northern and Southern Hemispheres. There are only 30 known plant species with such striking pattern, which may be seen as the largest possible disjunction. Accordingly, 20% of bipolar plant species belong to genus *Carex*. On the other hand, *Carex* section *Spirostachyae* (Drejer) L.H. Bailey (subgenus *Carex*) is composed of ca. 40 species (Fig. 3 G-L) mainly distributed in the Mediterranean Basin, Europe and Eastern tropical Africa (Fig. 5). Following the molecular phylogeny, two subsections were recognised, namely *Spirostachyae* (11 spp.) and *Elatae* (Kük.) Luceño and M. Escudero (29 spp.; Fig. 4). Both have a centre of diversification in the Mediterranean region (Fig. 5 A,B, respectively), while subsection *Elatae* displays an additional centre of species diversity in the mountainous region of Eastern tropical Africa (Fig. 5B). In addition, sect. *Spirostachyae* includes some widely disjunct species growing in South America, South Africa, Australia, and the oceanic archipelagos of Macaronesia, Tristan da Cunha, Bioko Island and Mascarene Islands (Fig. 5A).

### 3.2 Methods

Molecular phylogenies were reconstructed for each of the studied groups based on nuclear and plastid DNA regions, with maximum parsimony and Bayesian inference criteria. In Resedaceae, a first phylogeny based on nuclear ribosomal DNA (nrDNA) ITS and plastid *trnL-F* sequences tested the monophyly of the family and established its main lineages (Martín-Bravo et al., 2007). Species diversity and endemism, together with the distribution of the main lineages and their phylogenetic relationships, were analysed to obtain biogeographic insights in Resedaceae (Martín-Bravo et al., 2007). The basic phylogenetic framework subsequently enabled the development of further studies focusing on different lineages which displayed interesting evolutionary or biogeographic features (*Oligomeris*, Martín-Bravo et al., 2009; *Reseda* section *Glaucorese* DC., Martín-Bravo et al., 2010). For both groups, phylogeographic analyses were performed, including the reconstruction of haplotype networks with statistical parsimony, using nrDNA ITS and cpDNA *trnL-F* and *rps16* sequences. Penalized likelihood analyses were performed to estimate divergence

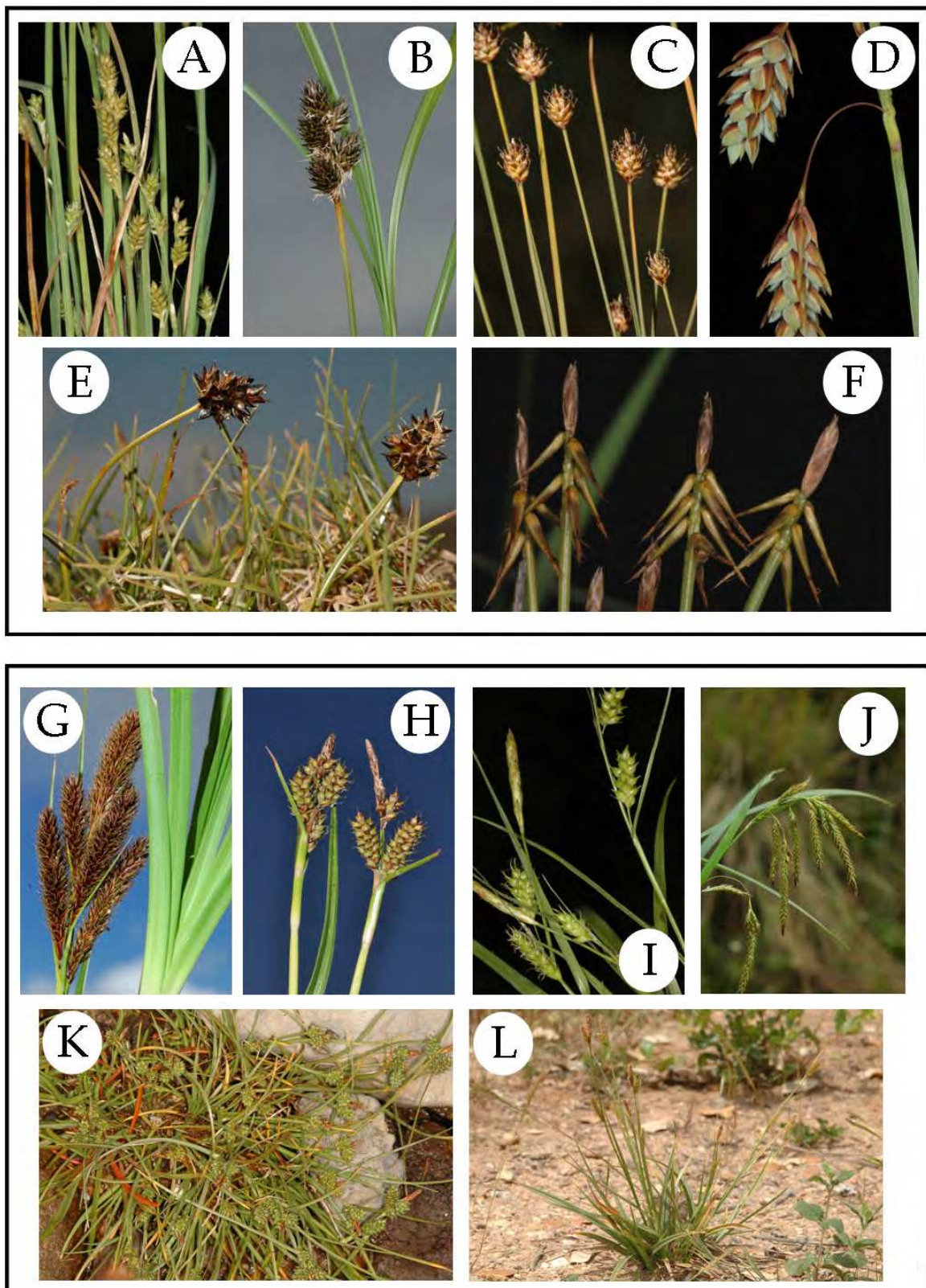


Fig. 3. Representatives of the studied *Carex* species. Upper box, bipolar sedges: A) *C. canescens*; B) *C. macloviana*; C) *C. arctogena*; D) *C. magellanica*; E) *C. maritima*; F) *C. microglochin*. Lower box, *Carex* sect. *Spyrostachyae*: G) *C. borbonica*; H) *C. lainzii*; I) *C. punctata*; J) *C. greenwayi*; K) *C. extensa*; L) *C. helodes*.



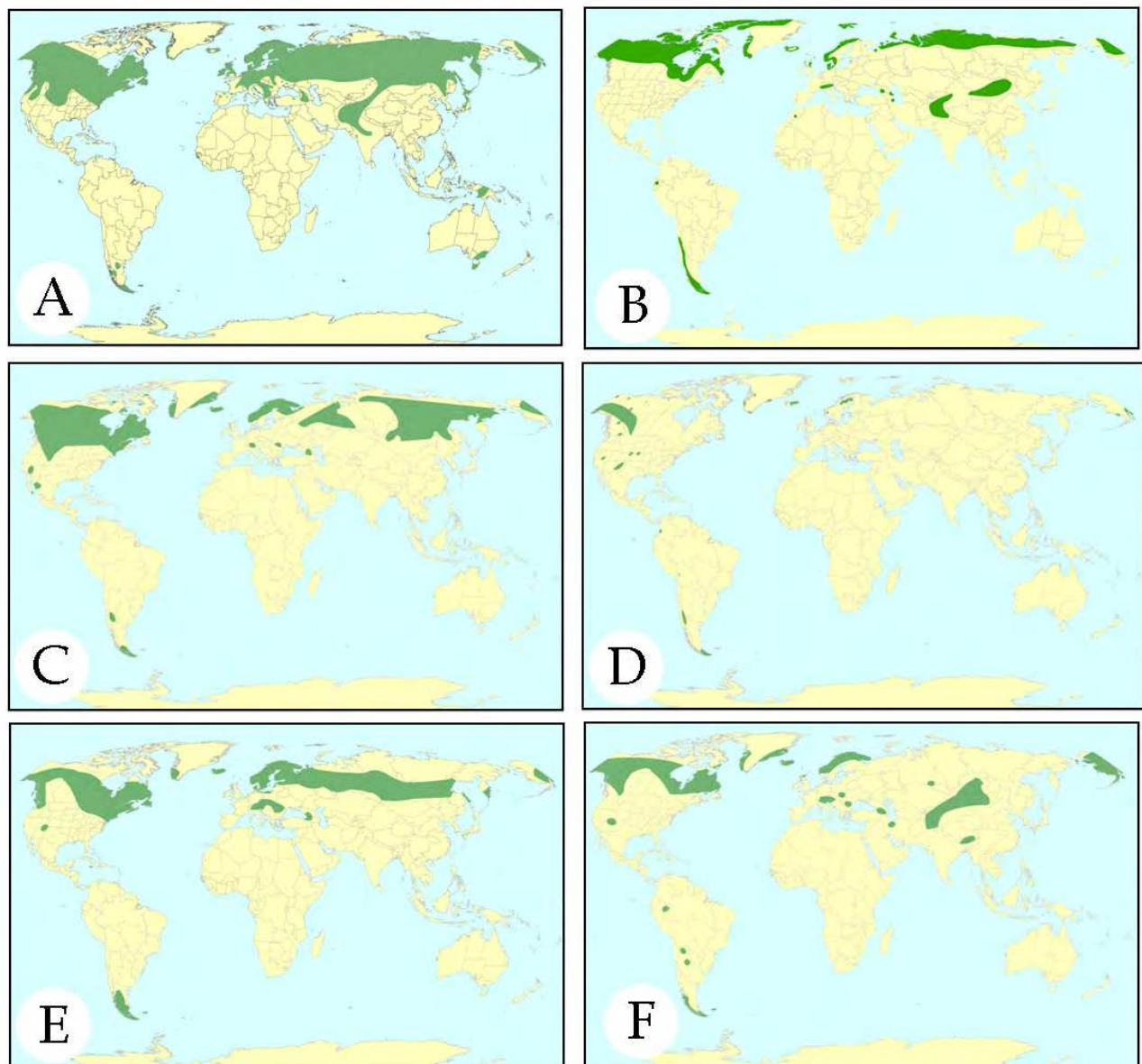


Fig. 4. Approximate distribution of bipolar *Carex* species: A) *C. canescens*; B) *C. maritima*; C) *C. arctogena*; D) *C. macloviana*; E) *C. magellanica*; F) *C. microglochin*.

times, based on ITS and cpDNA sequences (*rbcl*, *matK*, *trnL-F*). Additionally, in *Oligomeris*, an independent molecular clock approach was performed, namely a test of vicariance based on nucleotide substitution rates. Finally, in *Reseda* sect. *Glaucoriseda*, a selected set of ITS sequences was cloned to investigate the origin of intra-individual polymorphisms.

In bipolar *Carex* species, molecular phylogenies based on nuclear ribosomal DNA (ITS) and plastid (*rps16*) sequences tested the monophyly of five of the six bipolar *Carex* species; haplotype network reconstructions based on the statistical parsimony method and using cpDNA (*rps16*) sequences were used to analyse the genetic-geographic structure within them (Escudero et al., 2010a). In *Carex* sect. *Spirostachyae*, molecular phylogenies based on nuclear ribosomal DNA ITS and plastid 5' *trnK* intron sequences tested the monophyly of the section and established its main lineages (Escudero et al., 2008a; Escudero & Luceño, 2009). Subsequently, several studies addressing biodiversity and biogeographic questions

for sect. *Spirostachyae* as a whole were performed, using ancestral area reconstruction (dispersal-extinction-cladogenesis and stochastic methods using maximum likelihood and Bayesian inference approaches, respectively) and estimation of times of diversification (penalized likelihood and parametric uncorrelated log-normal methods using maximum likelihood and Bayesian inference approaches, respectively; Escudero et al., 2009, 2010b). More specifically, different lineages which displayed interesting phylogeographic patterns were studied with AFLP and SSR fingerprinting data, in addition to DNA sequences (*C. helodes* Link, Escudero et al., 2008b; *C. extensa* Good. and allies, Escudero et al., 2010c). For both groups, phylogeographic analyses were performed, including the reconstruction of haplotype networks with statistical parsimony using cpDNA sequences (*rps16* and 5′*trnK* intron for *C. helodes* and *C. gr. extensa*, respectively). Both penalized likelihood and parametric uncorrelated log-normal analyses were performed to estimate divergence times in *C. gr. extensa*, based on ITS and cpDNA sequences (5′*trnK* intron).

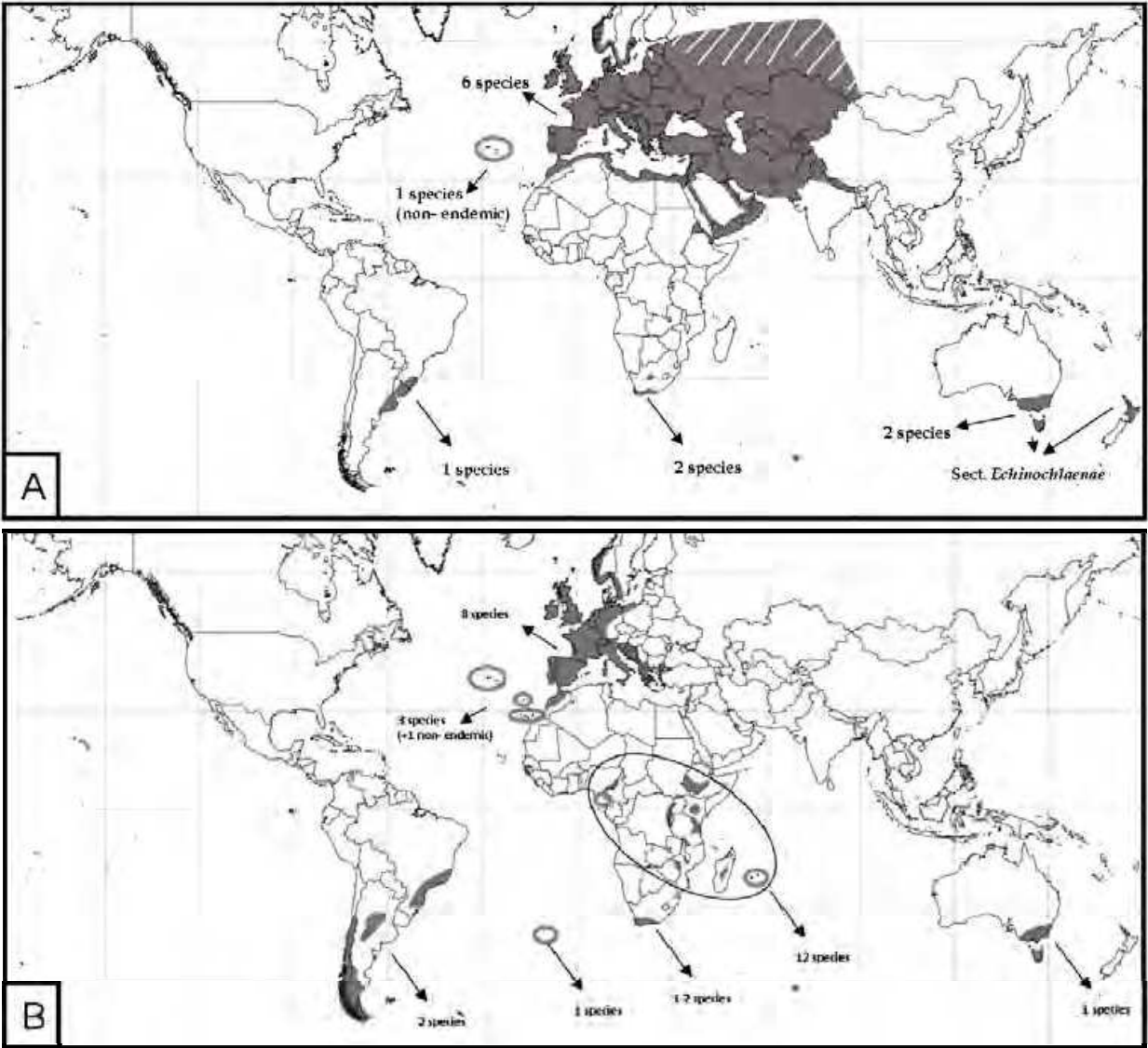


Fig. 5. Approximate distribution of *Carex* sect. *Spirostachyae* and species richness in each of the main distribution areas (see details in Escudero et al., 2009): A) Subject. *Spirostachyae*; B) Subject. *Elatae*.

### 3.3 Main findings and discussion

#### 3.3.1 Patterns of distribution and centres of diversification

In Resedaceae, the Iberian Peninsula and NW Africa harbour one endemic (*Reseda* sect. *Glaucorese*) and two subendemic (genus *Sesamoides* and *Reseda* sect. *Leucorese* DC.) lineages. On the other hand, sect. *Reseda* appears to have diversified mainly in the Middle East. Section *Phyteuma* Lange is mostly composed of regional endemics restricted to either the Western or the Eastern Mediterranean regions, including such East-West disjunction between closely related species (*R. media* Lag. – *R. orientalis* (Müll. Arg.) Boiss; Martín-Bravo et al., in prep.). In sect. *Phyteuma*, the inferred speciation rate in the Eastern Mediterranean could be significantly higher than in the Western; likewise, dispersal from the Eastern to the Western Mediterranean appears to be predominant than the contrary (Martín-Bravo et al., in prep.). This biogeographical E-W Mediterranean pattern, repeatedly found at different taxonomic levels within Resedaceae (genera, sections and species) could be related to two major, disjunct centres of diversification at both sides of the Mediterranean. This also has been reported for other plant groups at different taxonomic levels (Plumbaginaceae subfamily Staticoideae, Lledó et al., 2005; *Cuminum*, Davis & Hedge, 1971; *Hedera*, Valcárcel & al., 2003; *Buxus balearica*, Rosselló et al., 2007; *Carex extensa*, Escudero et al., 2010c; *Erophaca baetica*, Casimiro-Soriguer et al., 2010; *Microcnemum coralloides*, Kadereit & Yaprak, 2008). Accordingly, both areas are considered melting pots of plant diversity and endemism (Médail & Quézel, 1997, 1999) within the Mediterranean Basin hotspot (Myers et al., 2000), and traditionally have been seen as critical for the diversification of Mediterranean flora. In contrast, non-Mediterranean Europe displays a low number of Resedaceae taxa, of which most are ruderal and widespread *Reseda* species (Martín-Bravo et al., 2007). This distribution pattern in Resedaceae leads us to propose a general scenario of glacial refugia and diversification in the Western and Eastern regions of the Mediterranean (Hewitt, 1996, 2001; Médail & Diadema, 2009; Taberlet et al., 1998). Species with greater colonization and dispersal ability could have postglacially recolonized Europe from those refugia. In areas of high diversification like the Iberian Peninsula and NW Africa (including the Canary Islands) geographical isolation could be regarded as an important driver of speciation (Martín-Bravo et al., 2010), probably as a result of the climatic, edaphic and topographic heterogeneity of these regions (Cowling & al., 1992, 1996; Martín-Bravo et al., 2007). Northeastern tropical Africa and the southern Arabian Peninsula feature an extraordinary endemism degree for Resedaceae (ca. 80%; Martín-Bravo et al., 2007). Two of the three *Caylusea* species and all *Reseda* species (nine) are endemic there. In addition, this region is clearly the center of diversity of genus *Ochradenus*, harbouring eight of its nine species, of which six are endemic. Active speciation processes have been related with the aridification of this area during the Pleistocene (Cane & Molnar, 2001; Chiarugi, 1933; Demenocal, 1995; Quézel, 1978), as well as with its topographic and geologic complexity. Genus *Reseda* appears to have diversified preferentially in the horn of Africa (six endemics), whereas *Ochradenus* displays a greater number of endemic species (four) in the southern Arabian Peninsula (Martín-Bravo et al., 2007).

As already pointed out, *Carex* is by far the largest angiosperm genera in the temperate and cold regions of the Northern Hemisphere. Interestingly, it displays an inverse latitudinal gradient of species richness (Hillebrand, 2004; Kaufman & Willig, 1998). This feature suggests that historical cold periods could have promoted *Carex* diversification (Escudero et



al., in prep.). Bipolar *Carex* species are an interesting example of this distribution pattern in cold regions of the Northern Hemisphere. In contrast, *Carex* sect. *Spirostachyae* is a very peculiar group within the genus *Carex*, as it preferentially grows in warmer regions, and accordingly, is mainly distributed in the Mediterranean Basin and Eastern tropical Africa. Both subsections within *Spirostachyae* have a center of diversification in the Mediterranean region (with six of 11 species in subsect. *Spirostachyae*, and eight of 29 in subsect. *Elatae*; Fig. 5), while subsection *Elatae* displays an additional centre of species diversity in the mountainous region of Eastern tropical Africa (10 of 29 species; Fig. 5B). In addition, sect. *Spirostachyae* includes some widely disjunct species growing in remote regions in the world (Fig. 5A). On one hand, subsect. *Elatae* has disjunct species in South America (2 spp.), South Africa (1-2 spp.), Australia (1 sp.), and the oceanic archipelagos of Macaronesia (3 spp.), Tristan da Cunha (1 sp.), and Mascarene Islands (2 spp.). On the other hand, subsect. *Spirostachyae* includes disjunct species in South America (1 sp.), South Africa (2 spp.), Australia (2 spp.), and the archipelagos of Macaronesia (3 endemics and one species also distributed in the continental Old World). Interestingly, the section *Echinochlaenae* T. Holm (ca. 30 spp.; subendemic of the Northern Island of New Zealand, with ca. 2 spp. growing in Australia) forms a monophyletic group together with the Australian species of subsect. *Spirostachyae* (personal communication from Dr. Marcia Waterway, McGill University, Montreal, Quebec, Canada).

### 3.3.2 Range disjunctions: Long-distance dispersal or vicariance?

Our study groups show interesting patterns of disjunction at very different geographic scales (Figs. 2, 4, 5). Phylogenetic and phylogeographic analyses, molecular dating of lineage divergence, palaeogeological/climatic data, and ancestral range reconstruction (see methods in 3.2) were variously used to try to answer one of the prevailing questions in plant biogeography: the explanation of the causes of such disjunctions.

#### 3.3.2.1 Old - New World disjunctions

In Resedaceae, one species in genus *Oligomeris* (*O. linifolia*) is widespread in desert and arid areas of the Old World (N Africa - SW Asia), and also includes disjunct populations in the New World (SW North America), constituting the most remarkable disjunction within the family (Fig. 2). Two examples of Old - New World disjunctions between closely related species may be found in *Carex* sect. *Spirostachyae*: *C. extensa* (subsect. *Spirostachyae*) and *C. punctata* Gaudin (subsect. *Elatae*) grow in the Mediterranean Basin, Europe and SW Asia, while their sister species *C. vixdentata* (Kük.) G.A. Wheeler and *C. fuscula* D'Urv - *C. catharinensis* Boeck., respectively, occur in Central and Southern South America (Fig. 5).

This pattern of trans-oceanic disjunction, rarely found at the species level in plants, has been traditionally explained by vicariance hypotheses dating back at least to the Miocene (ca. 20 m.a; Axelrod, 1975; Stebbins & Day, 1967; Tiffney, 1985). More recently, molecular dating has explained this pattern of disjunction at the family and genus level, favouring long-distance dispersal in some cases (i.e. *Erodium*, Fiz et al., 2010; *Thamnosma*, Thiv et al., 2011) and vicariance in others (reviewed in Wen & Ickert-Bond, 2009). In our *Oligomeris* study, relatively recent estimates of divergence time for *O. linifolia* (Upper Pleistocene), the low level of genetic differentiation between the disjunct populations, and the distribution of the rest of the family, suggests a long-distance dispersal event from the Old World, probably



occurred during the Quaternary, to account for this disjunction (Martín-Bravo et al., 2009). Our hypothesis is congruent with the results obtained for other species from arid regions that display a similar disjunction (*Senecio mohavensis*, Coleman et al., 2003; *Plantago ovata*, Meyers & Liston, 2008). These studies also have estimated Pleistocene as the temporal framework and the same direction of the dispersal event (from the Old to the New World). However, both species have epizoochoric dispersal syndromes (Coleman et al., 2003; Meyers & Liston, 2008), while *Oligomeris* lacks apparent specific mechanisms for long-distance dispersal. Results from our *Spirostachyae* study are mostly congruent to those from *Oligomeris*. Firstly, estimation of divergence times in sect. *Spirostachyae* also discards a vicariance pattern and supports trans-hemisphere, Old to New World, long-distance dispersal. In addition, as in *Oligomeris*, the *Carex* species studied apparently lack specific mechanisms for long-distance dispersal. Nevertheless, estimation of the split between Old and New World species are not as recent as in *Oligomeris*, dating back to Pliocene times (Escudero et al., 2009, 2010b).

### 3.3.2.2 Northern – Southern Hemisphere disjunctions

In Resedaceae, two *Oligomeris* species (*O. dipetala*, *O. dregeana*) are endemic to SW Africa, in contrast to the mostly Mediterranean distribution of the Resedaceae (Fig. 2). Many species show a disjunct distribution between arid regions of Southern and Northern Africa (Goldblatt, 1978; Thulin, 1994; de Winter, 1971). Both dispersalist and vicariance hypotheses have been invoked to explain this pattern of disjunction (i.e. Beier et al., 2004; Thiv et al., 2011; Thulin, 1994). The latter has been based on the presence of an arid corridor through Eastern Africa which intermittently connected Northern – Southern Africa during the Pliocene – Pleistocene (Jürgens, 1997; Verdcourt, 1969; van Zinderen Bakker, 1978), although the exact age of this corridor is still disputed (Thiv et al., 2011). These palaeoclimatic data, together with our Lower Pleistocene time estimates for the origin of genus *Oligomeris* (Martín-Bravo et al., 2009) does not allow us to clarify the process involved in the origin of the SW African endemics.

As stated above, the genus *Carex* includes six of the 30 known plant species which display a bipolar disjunction (Moore & Chater, 1971). This has traditionally been one of the most intensively studied patterns of disjunct distributions, and both long-distance dispersal and vicariance hypotheses have been proposed (Moore & Chater, 1971, Vollan et al., 2006). The later were based on the presence of trans-tropical land bridges through mountain ranges during the Mesozoic age (250 - 65 m.a; du Rietz, 1940). Phylogenetic relationships and the low level of genetic differentiation among Northern-Southern populations of *Carex* species suggest long-distance dispersal as the most plausible cause of the bipolar disjunction for the five sampled species (all except for *C. arctogena*, not included in Escudero et al., 2010a). In addition, haplotype genealogical relationships point to a southward direction of dispersal in three species (*C. macloviana*, *C. magellanica* and *C. canescens*; Escudero et al., 2010a). Nevertheless, the timing of these bipolar disjunctions and the alternative dispersal hypotheses (i.e. direct long-distance dispersal or mountain hopping; Escudero et al., 2010a) involved in their origin remain to be investigated. A very recent study of the bipolar disjunction displayed by genus *Empetrum* (Popp et al., 2011; see also Donoghue, 2011) also explained it with a North to South long-distance dispersal colonization. In addition, they dated the event to Pleistocene times and postulated that direct dispersal rather than mountain hopping was at the origin of the disjunction. On the other hand, *Carex* sect.

*Spirostachyae* shows an interesting pattern of Northern - Southern Hemisphere disjunctions. In addition to the above cited species in South America (see Old - New World disjunctions), there are two species in South Africa (*C. ecklonii* Nees and *C. burchelliana* Boeck.) whose origin, according to ancestral range reconstruction, may be placed in the Northern Hemisphere Old World (ancestors of *C. gr. extensa* and *C. gr. distans*, respectively; Escudero et al., 2009). Estimations of times of diversification discard a vicariance process, and indicate that the most plausible hypothesis to explain these disjunctions is also North to South long-distance dispersal in Late Miocene - Pliocene times (Escudero et al., 2009, 2010b).

### 3.3.2.3 Colonization of continental and oceanic archipelagos

Despite the Resedaceae and *Carex* sect. *Spirostachyae* apparently lack specific mechanisms for long-distance dispersal, they have successfully colonized various continental and oceanic archipelagos. *Oligomeris linifolia*, whose trans-oceanic disjunction has already been commented above, grows in many islands or archipelagos throughout its large range (Fig. 2B), including most islands off the Californian coast, the Eastern Canary Islands and islands in the Persian Gulf (Martín-Bravo et al., 2009). Many of these islands are of oceanic origin and their indigenous floras a consequence of dispersal from mainland. Moreover, some of them are situated a considerable distance from the mainland, such as the Canary Islands (ca. 100 km), the Channel Islands (20-100 km), and Guadalupe Island (260 km). Therefore, *O. linifolia* seems to have great dispersal and colonization ability, despite its unassisted dispersal syndrome. Other organisms with apparent low dispersal ability display a similar pattern of oceanic dispersal (review in de Queiroz, 2005).

At least four independent long-distance dispersal events could have been involved in the colonization of the oceanic Canary Islands by the four species of the family growing there (the widespread *Oligomeris linifolia* and *Reseda luteola* L., and the endemic *R. crystallina* Webb & Berthel. and *R. scoparia* Willd.), which are placed in distinct clades of the phylogeny (Martín-Bravo et al., 2007). The origin of the Canarian endemic *R. crystallina* could have taken place following dispersal from NW Africa, as inferred from its close phylogenetic relationship with the NW African *R. lutea* subsp. *neglecta* (Müll. Arg.) Abdallah & de Wit (Martín-Bravo et al., 2007). *Carex* sect. *Spirostachyae* is represented in Macaronesian archipelagos by three endemics from subsect. *Elatae*, *C. perraudieriana* Gay in Canary Islands, *C. lowei* Bech. in Madeira and *C. hochstetteriana* Gay in Azores, as well as by the presence of two widespread species, *C. extensa* in subsect. *Spirostachyae* and *C. punctata* in subsect. *Elatae*. Estimation of species diversification times in sect. *Spirostachyae* support a fairly old colonization of Macaronesia by the endemic species, probably predating Pliocene, and recent colonization of the widespread species (Escudero et al., 2009, 2010b). Phylogenetic relationships indicate multiple colonization events although it is difficult to know the exact number of colonizations (at least three; Escudero et al., 2009). In Macaronesia, a single dispersal event and subsequent colonization has usually been reported for taxa lacking specific dispersal syndromes, whereas recurrent colonization has rarely been reported for such plants (Vargas, 2007). In contrast, multiple colonizations have been frequently proposed for taxa with specific dispersal mechanisms (endozoocory: *Hedera*, *Ilex*, *Juniperus*, *Olea*; hidrocoory: *Euphorbia*, *Lavatera*; reviewed in Vargas, 2007, but see *Cistus*, Guzmán & Vargas, 2009a).

Likewise, two different allopatric speciation processes could have taken place in the colonization of Socotra archipelago by Resedaceae, represented by two phylogenetically distinct endemics, *Reseda viridis* Balf. f. and *Ochradenus socotranus* A.G. Mill. (Martín-Bravo et al., 2007). Socotra is of continental origin, but has remained isolated from continental masses for a long geologic term (18 - 15 m.a; van Damme, 2009; Fleitmann et al., 2004). Its age, together with the estimated Miocene origin of Resedaceae (10 - 16 m.a; Martín-Bravo et al., 2009, 2010), and the relatively low genetic differentiation between the endemics and their closest relatives, point again to independent long-distance dispersal events to account for the colonization of Socotra.

The colonization of the Atlantic archipelago of Tristan da Cunha archipelago (*C. thouarsii* Carmichael), and of the Mascarene Islands in the Indian Ocean (*C. boryana* Schkuhr and *C. borbonica* Lam.), seems to be recent (Escudero et al., 2009, 2010b). Specifically, low levels of genetic differentiation with their most closely related continental species, lead to infer relatively recent long-distance dispersal events from Western South America (*C. fuscula* – *C. catharinensis*) and Eastern tropical Africa (tropical African group of subsect. *Elatae*) to explain the colonization of Tristan da Cunha Archipelago Island and Mascarene islands, respectively (Escudero et al., 2009, 2010b). Plant colonization of Tristan da Cunha Archipelago has been scarcely study, and as far as we know, no similar pattern of colonization (dispersal from Western South America) has been previously described for angiosperms. Nevertheless, long-distance dispersal from Africa to Tristan da Cunha archipelago has been already proposed (Anderson et al., 2001; Richardson et al., 2003). On the other hand, our data support a single colonization of the Mascarene archipelago from Eastern tropical Africa or Madagascar. Uncertainty about the presence of sect. *Spirostachyae* in Madagascar does not allow us to clarify between both possibilities.

#### 3.3.2.4 Ibero-North African disjunctions across the strait of Gibraltar

The Iberian Peninsula and NW Africa have close biogeographic affinities (Médail & Quézel, 1997). The Ibero-North African floristic element is well represented in the flora of the Iberian Peninsula, especially in its southern part (Blanca et al., 1999). Thus, southern Iberia and northern Morocco share about 75% of 3,500 species (Valdés, 1991), with more than 500 endemics (Quézel, 1978). The two regions were connected from the end of the Miocene to the upper Pliocene due to the partial desiccation of the Mediterranean Sea following an increase in aridity (Messinian salinity crisis, 5.9-5.3 million years ago; Hsü et al., 1977; Duggen et al., 2003; Rouchy & Caruso, 2006), allowing contacts between the floras of the two continents.

*Reseda battandieri* Pit. is a Moroccan endemic species within the otherwise Iberian section *Glaucoredeseda*. Pleistocene divergence times estimated for sect. *Glaucoredeseda* and *R. battandieri* (Martín-Bravo et al., 2010) are later than the Mio-Pliocene opening of the Strait of Gibraltar (ca. 5.3 m.a; Krijgsman, 2002). This fact, together with genealogical relationships of haplotypes, suggests dispersal from the Iberian Peninsula across the Strait of Gibraltar during the Pleistocene, to account for the colonization of NW Africa by sect. *Glaucoredeseda* and the allopatric differentiation of *R. battandieri* (Martín-Bravo et al., 2010).

*Carex helodes* (sect. *Spirostachyae*) is an endemic species from SW Iberian Peninsula and Northern Morocco. Nuclear and plastid sequences, AFLPs and cytogenetic counts demonstrate that European and African populations constitute two independent lineages,

although with low genetic divergence between them (Escudero et al., 2008b). Genealogical relationships of haplotypes and the pattern of genetic diversity suggest dispersal from the Iberian Peninsula into NW Africa, probably later than the Mio-Pliocene opening of the Strait of Gibraltar (ca. 5.3 m.a; Krijgsman, 2002), and subsequent differentiation of Moroccan populations (Escudero et al., 2008b).

These results from *Reseda* and *Carex* underline the importance of the Strait of Gibraltar as a barrier to plant gene flow, although its specific role greatly depends on the study group. In most cases, a certain degree of differentiation at the specific or population level is observed, whereas continuity in the genetic structure has been reported in a few cases (review in Rodríguez-Sánchez et al., 2008). Overall, results from studies of other plant groups point to a dispersal rather than a vicariance pattern to explain Ibero-North African disjunctions (e.g. Guzmán & Vargas, 2009b; Jiménez-Mejías et al., 2011; Rodríguez-Sánchez et al., 2008; Rubio de Casas et al., 2006).

### 3.3.2.5 Ecological vicariance

Four of the five species in *Reseda* sect. *Glaucoreda* (*R. complicata* Bory, *R. glauca* L., *R. gredensis* (Cutanda & Willk.) Müll. Arg. and *R. virgata* Boiss. & Reuter) are endemics with an allopatric distribution in the high mountain ranges and plateaus of the Iberian Peninsula. We studied the possible correlation between Quaternary glaciations, historical range dynamics and speciation processes (Martín-Bravo et al., 2010). Molecular dating points to a late Pleistocene diversification of sect. *Glaucoreda*, which together with the current distribution of endemics and their cytogenetic features, suggest an ecological vicariance hypothesis, characterised by the interglacial range fragmentation of an ancestral species and subsequent allopatric speciation (Martín-Bravo et al., 2010). Ecological specialization in different kind of substrates could have acted in concert with geographical isolation to promote morphological differentiation and subsequent speciation (Dixon et al., 2007; Martín-Bravo et al., 2010) in the different Iberian species of sect. *Glaucoreda*. The clear morphological differences between sect. *Glaucoreda* species (Abdallah & de Wit, 1978; Martín-Bravo, 2009; Valdés Bermejo, 1993), coupled with the low level of molecular divergence among them, lead us to suggest that phenotypic has been faster than genotypic differentiation in sect. *Glaucoreda*, as suggested for other Resedaceae genera (Martín-Bravo et al., 2007). In summary, our results lend support to the important role of range shifts induced by Quaternary climatic oscillations in the diversification of European mountain plant groups.

Within *Carex* sect. *Spirostachyae*, subsect. *Elatae* shows an interesting pattern of species distribution with two disjunct centres of diversification, one in the Mediterranean and the second in the mountains of Eastern tropical Africa (Cronk, 1992; Escudero et al., 2009). Tropical African species of subsect. *Elatae* might have been abundant in subtropical and tropical African woodlands until the Late Pliocene, when these habitats were extensive (Cronk, 1992). Subsequently, these habitats were dramatically reduced during the Pleistocene aridification of Africa (Cronk, 1992), probably entailing extinction of many populations of these species. The Miocene origin estimated for this group (Escudero et al., 2009, 2010b) supports an ecological vicariance hypothesis in which the general cooling and aridification of Africa and the formation of Sahara Desert during the Late Pliocene-Pleistocene could have interrupted a previously continuous range. Subsequently, allopatric



speciation processes were probably responsible for the diversification of subsect. *Elatae* (Escudero et al., 2009).

4. Conclusions

Our biogeographic studies in Resedaceae and *Carex* provide examples of how the development of molecular biology and bioinformatics from the end of the XXth century has contributed to a revolution in the field of evolutionary biology, and, specifically, in biogeography. These advances have enabled us to gain insights into many long-standing questions in plant biogeography, like the location of ancestral areas and centers of diversification, the processes behind remarkable range disjunctions (vicariance vs. dispersal), and the important role of geography in plant evolution and biodiversity. With respect to range disjunctions, our results point to the outstanding importance of long-distance dispersal events rather than vicariance to explain different patterns of plant disjunction at diverse geographic scales, independently of the presence of specific mechanisms for long-distance dispersal. Remarkably, at least 23 long-distance dispersal connections (15 in *Carex* and 8 in Resedaceae) were inferred in our study groups (Fig. 6). We provide several documented examples of allopatric speciation, which confirm geographical isolation as one of the most important drivers of plant evolution. Geographical, coupled with reproductive isolation among populations, may lead to genetic divergence and, eventually, to speciation when gene flow is precluded. Ecological vicariance induced by range shift dynamics caused by climatic changes during Pliocene and Pleistocene also promoted speciation events and deeply shaped the current genetic structure of many species.

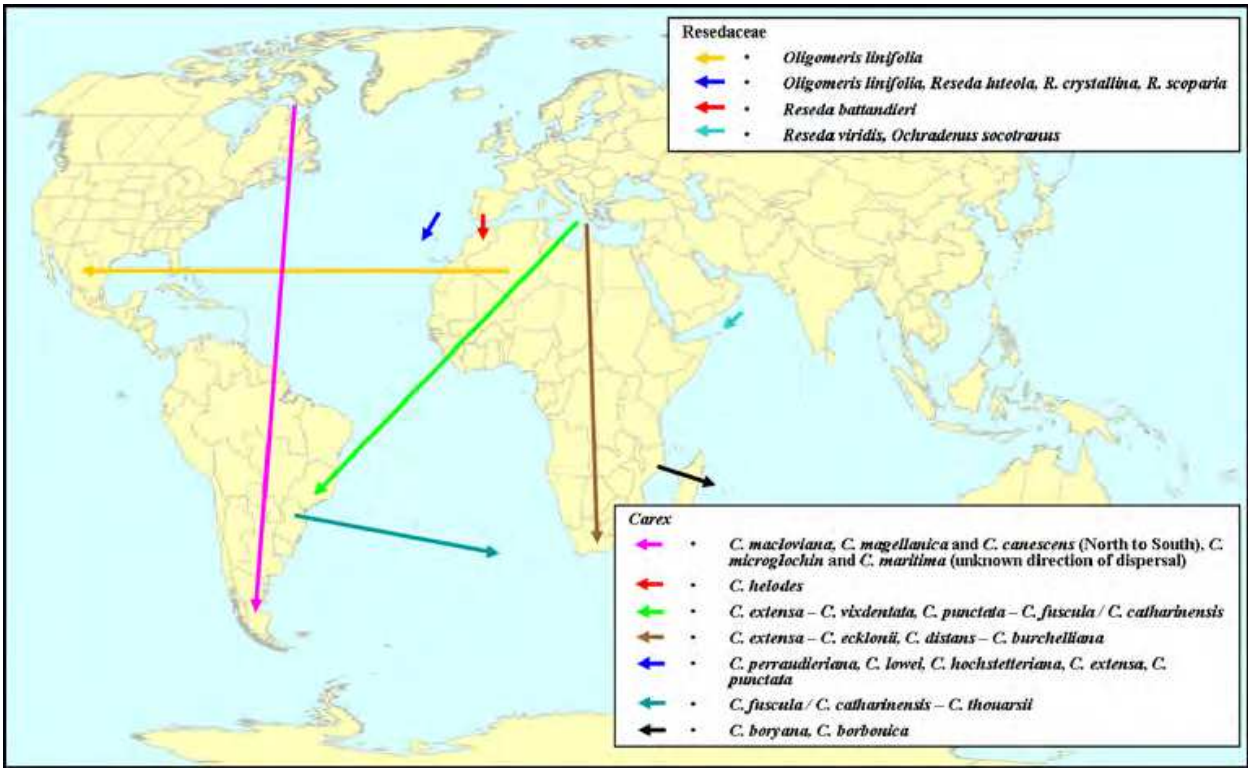


Fig. 7. Documented examples of long-distance dispersal connections inferred in our study groups (Resedaceae and *Carex*).

## 5. Acknowledgments

We thank Dr. M. Luceño, J.M. André, A. Al-Sirhan and P. Auroousseau for granting permission to publish some of the photographs included in this chapter, T. Villaverde for comments on the manuscript, and E. Maguilla for helping with the distribution map of bipolar sedges.

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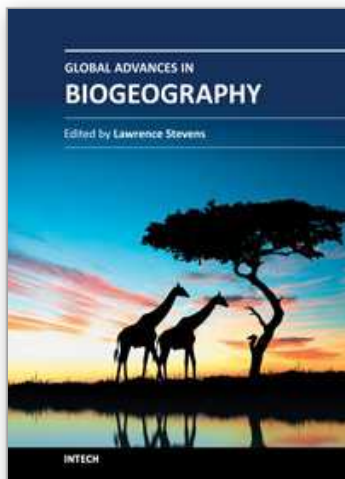
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## **Global Advances in Biogeography**

Edited by Dr. Lawrence Stevens

ISBN 978-953-51-0454-4

Hard cover, 360 pages

**Publisher** InTech

**Published online** 30, March, 2012

**Published in print edition** March, 2012

Global Advances in Biogeography brings together the work of more than 30 scientific authorities on biogeography from around the world. The book focuses on spatial and temporal variation of biological assemblages in relation to landscape complexity and environmental change. Global Advances embraces four themes: biogeographic theory and tests of concepts, the regional biogeography of individual taxa, the biogeography of complex landscapes, and the deep-time evolutionary biogeography of macrotaxa. In addition, the book provides a trove of new information about unusual landscapes, the natural history of a wide array of poorly known plant and animal species, and global conservation issues. This book is well illustrated with numerous maps, graphics, and photographs, and contains much new basic biogeographical information that is not available elsewhere. It will serve as an invaluable reference for professionals and members of the public interested in global biogeography, evolution, taxonomy, and conservation.

### **How to reference**

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Santiago Martín-Bravo and Marcial Escudero (2012). Biogeography of Flowering Plants: A Case Study in Mignonettes (Resedaceae) and Sedges (Carex, Cyperaceae), Global Advances in Biogeography, Dr. Lawrence Stevens (Ed.), ISBN: 978-953-51-0454-4, InTech, Available from:  
<http://www.intechopen.com/books/global-advances-in-biogeography/biogeography-of-flowering-plants-a-case-study-in-mignonettes-resedaceae-and-sedges-carex-cyperaceae>

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