
Modified Dispersal-Related Traits in Disjunct Populations of Bird-Dispersed Frangula Alnus (Rhamnaceae): A Result of Its Quaternary Distribution Shifts?
Author(s): Arndt Hampe and Franz Bairlein
Source: *Ecography*, Vol. 23, No. 5 (Oct., 2000), pp. 603-613
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3683294

ECOGRAPHY 23: 603–613. Copenhagen 2000

Modified dispersal-related traits in disjunct populations of bird-dispersed *Frangula alnus* (Rhamnaceae): a result of its Quaternary distribution shifts?

Arndt Hampe and Franz Bairlein

Hampe, A. and Bairlein, F. 2000. Modified dispersal-related traits in disjunct populations of bird-dispersed *Frangula alnus* (Rhamnaceae): a result of its Quaternary distribution shifts? – Ecography 23: 603–613.

Many European tree species survived Pleistocene glaciations in Mediterranean refugia and rapidly recolonized temperate Europe afterwards. Inter- and postglacial migration processes are assumed to have catalized evolutionary optimizations of dispersal-related traits, but up to now empirical evidence is lacking in vertebrate-dispersed plants. We investigated if south Iberian glacial relict and central European "colonizer" populations of the bird-dispersed tree *Frangula alnus* have experienced differentiations of dispersal-related traits which increase the mobility of northern populations. A comparison of lifetime reproductive strategy, disperser guilds, ripening phenology, and fruit design revealed considerable differences. Compared to south Iberian conspecifics, central European plants were considerably smaller and experienced a highly accelerated generation turnover. In south Iberian populations seed dispersal was carried out almost completely by resident birds which occurred in constant abundances throughout the ripening season. In contrast, central European seeds were dispersed by migrants whose abundances changed considerably during the ripening season. Several bird species were involved in both study areas but rendered different importance for seed dispersal. The fruit ripening pattern was highly asynchronous throughout the ripening season in south Iberia, while central European trees showed a complex ripening sequence which resulted in a significant correlation between fruit abundance and changing disperser availability. Central European fruits were smaller and showed a considerably smaller seed load than south Iberian fruits, thus presumably being more attractive for their small-sized main dispersers (*Sylvia* warblers). Chemical analyses revealed significant differences in contents of water, glucose, fructose, proteins, ash, and phenolic compounds. The extensive differentiation of dispersal-related traits in *F. alnus* suggests that even weak selective pressures by frugivores may induce evolutionary adjustments of dispersal traits over large time scales. We suggest that the differences we observe today evolved during the species' distribution shifts in the Quaternary.

A. Hampe (arndt@cica.es) and F. Bairlein, Inst. für Vogelforschung "Vogelwarte Helgoland", An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany (present address of A. H.: Dept de Biologia Vegetal y Ecologia, Univ. de Sevilla, Apdo. 1095, E-41080 Sevilla, Spain).

Pollen records show that many European and North American tree species spread northward from their glacial refugia in several interglacial periods of the Quaternary and in the early Holocene, reaching average speeds of up to 2000 m yr^{-1} (Bernabo and Webb 1977, Huntley and Birks 1983). These rapid distribution shifts and related demographic processes (e.g. founder or hybridization events) are assumed to have increased rates of morphological and genetic differentiation (Hewitt 1988, Barton and Hewitt 1989, Huntley and Webb

Accepted 17 December 1999

ISSN 0906-7590

1989, Newton et al. 1999). Especially dispersal-related traits should have been optimized during the northward progressions, because high mobility provides elevated fitness within advancing or retreating populations (Bennett 1986, Clark 1998). Cwynar and MacDonald (1987) found more mobile diaspores in northern populations of the wind-dispersed *Pinus contorta*, but in vertebrate-dispersed plants evidence for adaptive adjustments of dispersal traits in northern "colonizer" populations is lacking.

Extensive research on mutualistic interactions between fleshy-fruited plants and their vertebrate dispersers does mostly not support hypotheses of a microevolutionary shaping of zoochorous dispersal traits by dispersal agents: fruit selection patterns by frugivores are weak (Jordano 1987, 1995a, b, Sallabanks 1993a, Willson and Whelan 1993, Fuentes 1995) and exert little influence on the overall fitness (Herrera 1988, Jordano 1989, Traveset 1994, Herrera et al. 1994). Dispersal traits are influenced by environmental and developmental constraints on flower and fruit structure (Gorchov 1985, Primack 1987, Debussche et al. 1987, Eriksson and Ehrlén 1991, 1998, Fuentes 1992, Chiarucci et al. 1993, Guitián 1998). Additionally, they seem to be evolutionarily conservative, since variation of fruit design is better explained by phylogenetic relations than by adaptive models (Bremer and Eriksson 1992, Herrera 1992, Jordano 1995b). Consequently, current adjustments between fleshy-fruited plants and frugivores are mostly interpreted as the result of a complex, multispecific "diffuse coevolution" (Janzen 1980, Herrera 1982, 1985) or of "ecological fitting" (Janzen 1985), a demographic process within plant communities which occurs virtually without adaptive adjustments of pre-existing dispersal traits (Herrera 1995).

Nevertheless, although it is a truism that historical events have shaped current plant traits (Newton et al. 1999), up to now no studies on vertebrate-dispersed plants have searched for intraspecific differentiations of dispersal traits on the background of postglacial migration processes. Pollen records show that the alder buckthorn *Frangula alnus* Miller was one of the first bird-dispersed woody plants that recovered much of temperate Europe from Mediterranean refugia in the early Holocene (Moe 1984). We studied Iberian glacial relict populations and central European "colonizer" populations of *F. alnus* and compared both lifetime reproductive strategy and dispersal-related characteristics presumably relevant for effective propagation. Our aim was to test whether the northern populations have developed adaptations to increase their spatial mobility by: 1) accelerating the generation turnover and 2) adjusting dispersal traits (ripening phenology and fruit design) to changing disperser guilds.

Natural history of the plant

The distribution of *F. alnus* covers most of temperate Europe and western Asia extending to central Britain and central Scandinavia in the north (Meusel et al. 1978). At the southwestern edge of its distribution it is represented by the subspecies *Frangula alnus baetica* (Rev. and Willk.) Rivas Goday, endemic of the southern Iberian Peninsula and northern Morocco (Valdés et al. 1987). Medán (1994) states that *F. alnus* was already present on the Iberian Peninsula before the onset of the Mediterranean climate in the Pliocene. Recent south Iberian populations can be assumed to be glacial relicts (Medán 1994). Pollen records show that the species reached south Scandinavia in the Allerod and was distributed over much of Europe in the Preboreal and Boreal (Moe 1984). *Frangula alnus* has been recently introduced into North America, is quickly expanding and becoming a pest in some regions (Taft and Solecki 1990, Catling and Porebski 1994).

In temperate Europe the nominate subspecies preferably grows on acid, moist soils and can build up plentyful populations in the understorey of light forests, at forest edges or on fens (Godwin 1936, 1943, Ellenberg 1996). The species is a typical woody pioneer during the succession of drained mires and conveyed wet meadows, being overgrown and substituted by forest vegetation. The south Iberian *F. alnus baetica* is restricted to locations with weak summer drought (Valdés et al. 1987). Its major populations grow in the understory of gallery forests along virtually yearround active creeks in the coastal mountain ranges of southern Andalusia.

Reproductive biology and organs of *F. alnus* have been described in detail by Meinhardt (1971) and Medán (1994). The entomophilous species produces blackish two- or three-seeded fruits, which are eaten almost exclusively by birds (unpubl., Kollmann and Pirl 1995).

Study areas

The central European part of the study was carried out between May and November 1996 in the "Rauhes Moor" nature reserve (427 ha, 20 m a.s.l., 54°5′N; 12°30′E, Mecklenburg-Vorpommern, NE Germany). Mean annual temperature is ca 7.9°C, precipitation is distributed more or less evenly throughout the year and averages 580 mm. The reserve covers a fen dominated by moist birch (*Betula pubescens* Ehrh.) forests with numerous clearings and meadows in various stages of succession. *Frangula alnus* is widespread on open sites throughout the reserve and by far the most abundant fleshy-fruited species in the area. Our study was conducted in two populations in the southern and western part of the reserve, which count with several hundred adult plants.

The south Iberian part of the study was conducted between May and September 1997 in the Sierra del Aljibe mountain range, 40 km northwest of Gibraltar (36°30′N; 5°35′W, Andalusia, S Spain). The annual temperature averages 16.6°C, rainfall concentrates in the winter months and amounts to 1220 mm. Our study covered three populations located in the Aljibe, Medio and Puerto Oscuro Valley within an altitudinal range between 350 and 700 m a.s.l. Each population consists of some hundred trees. They grow in 10–30 m broad gallery forests that are dominated by *Alnus glutinosa* (L.) Gaertn. and bear a high portion of caducifolious and lauriphyllous species (Medán 1994). This vegetation is surrounded by sclerophyllous Mediterranean scrub and light cork oak *Quercus suber* L. forest, which count with several fleshy-fruited shrubs. Nevertheless, only two of 17 species (*Smilax aspera* L. and *Rubus ulmifolius* Schott) ripened remarkable numbers of fruits during the study period.

Methods

Lifetime reproductive strategy

At both study sites we chose representative areas of *F. alnus* habitats and determined plant height, diameter of the main stem (at 0.6 m above ground level), and crop size of every *F. alnus* individual with ≥ 0.5 cm stem diameter. Dead trees were included. The measured stem diameters were correlated with absolute age after analyses of 50 dendrometer samples from each study site, respectively, collected within the plots studied in detail. The stem diameter reflects accurately the absolute age, because *F. alnus* does not reproduce vegetatively (unpubl., Godwin 1943, Medán 1994). One or two stem cores per individual were taken at 0.6 m above ground level, dried, treated with phloroglucinol, and annual rings were counted under a 10 × magnifier. We obtained reliable ring counts of 44 Iberian and 36 central European individuals, which were included in a linear regression analysis.

Disperser guilds

The frugivorous avifaunas were recorded throughout the ripening season using a point-count method (Bibby et al. 1992). Counts were performed every five days at 15 points and lasted five minutes per point. All birds within a radius of 50 m were recorded and assigned to one of three habitats (Table 1).

In both study areas we systematically observed eight fruiting *F. alnus* trees. The observations were separated in units of three to four hours. They were spread throughout the ripening season and covered one day (7.00–19.00) per single tree in central Europe, summing to a total of 96 h, and one day (8.00–21.30) per every two trees in south Iberia, summing to 54 h. During foraging visits (i.e. the arrival of a bird in the tree followed by obvious fruit foraging activity), we recorded the bird species and the number of fruits ingested (see Hampe and Bairlein 1999a for more details). Additional foraging records in the study areas were included in the analyses.

Dispersal traits

Prior to the ripening season we marked three branches on twenty central European and south Iberian trees, respectively, to monitor the fruit ripening phenology. Fruit counts were conducted every five days throughout the ripening season and a total of 5812 fruits (central Europe) and 4884 fruits (south Iberia) were monitored. We classified fruits as unripe, ripe, deterred (desiccated or damaged), and fallen off (pedicels of fallen ripe fruits remained and were removed during every count). We calculated the time span from the first ripe fruit until 50% of the individual fruit crop had ripened to compare the fruit ripening synchronization within and among trees. Additionally, we individually marked a number of recently pollinated flowers to assess the time required from pollination until fruit maturation.

Table 1. Habitats used by birds during point-counts; presence of *F. alnus*: a = abundant, s = sparse, – = absent.

Habitat	south Iberia	*Frangula*
gallery forest	dense, up to 15 m high decidous vegetation dominated by *Alnus glutinosa* and *Rhododendron ponticum*	a
oak wood	more or less dense sclerophyllous shrub layer and sparse tree layer up to 15 m, made up by *Quercus suber* or *Q. canariensis*	–
scrub	dense sclerophyllous shrub vegetation up to 5–6 m, dominated by *Viburnum tinus*, *Arbutus unedo* and *Phillyrea* spp.	–
	central Europe	
forest	8–15 m high, light birch forest, poorly developed understory and dense herb layer	–
forest edge	mixed tree and scrub layer of variable height and density, dominated by *Betula pubescens* and *Salix* spp.	s
scrub	more or less dense scrub formations mostly lacking overgrowing trees and narrow contact to closed forest	a

Table 2. Character of south Iberian and central European *F. alnus* populations; mean ± SD, maximum in parenthesis. Different letters represent highly significant differences ($p < 0.001$, U-test or χ^2-test).

	south Iberia	central Europe
n	234	154
tree height [m]	6.5 ± 2.4^{a} (14.0)	2.3 ± 0.7^{b} (6.5)[1]
stem no. per individual	1.4 ± 1.3^{a} (8)	3.7 ± 3.3^{b} (21)
diameter of main stem [cm]	9.7 ± 6.4^{a} (40.3)	2.7 ± 1.3^{b} (11.2)[1]
age [a]	25.2 ± 20.4^{a}	9.5 ± 4.1^{b}
age at first fruit reproduction [a]	20	5
adult trees [%]	66^{a}	83^{b}
fruiting trees [%]	57^{a}	75^{b}
crop size	2843 ± 3747^{a} (25 000)	833 ± 336^{b} (11 700)
dead trees [%]	11.1^{a}	17.5^{b}
nonadult fraction of dead trees [%]	57.7^{a}	3.7^{b}

[1] maximum measured outside the population sample studied in detail.

Table 3. Fruit ripening synchronization within and among individual trees. Test results for within-individual synchronization (t-test) are shown in the upper part of the table, results for among-individual synchronization (Levene's test on the homogeneity of variances) in the lower part.

	south Iberia	central Europe S1	central Europe S2
south Iberia	–	$p < 0.001$	$p = 0.27$
central Europe S1	$p < 0.001$	–	$p < 0.001$
central Europe S2	$p < 0.001$	$p < 0.001$	–

Fruit samples were collected individually from several trees, deep-frozen and stored at −18°C until morphometric and chemical analyses. Standard analytical methods were used (glucose and fructose: enzymatic method (Boehringer Mannheim), nitrogen: Kjeldahl, ash: 24 h incineration at 500°C, lipids: Soxleth, phenolic compounds: Price and Butler method).

Synchronization of fruit and disperser abundance

The relative importance of each bird species for the seed dispersal of *F. alnus* seeds was calculated. We developed an index that included both a quantitative and a qualitative dispersal component (Schupp 1993, Loiselle and Blake 1999): the species' contribution to the total fruit removal and its use of habitats suitable for *F. alnus* establishment. Its contribution to fruit removal (R) was computed by the percentage of recorded foraging visits multiplicated with the average number of fruits eaten per visit. Its habitat use (H) was obtained from the percentage of point-count records that were made in *F. alnus* habitats (see Table 1). The relative importance for seed dispersal (I) was then calculated for each species by:

$$I_i = \frac{R \times H}{\sum_{i=1}^{s} (R \times H)}$$

The overall disperser availability (D) at a given moment of the ripening season was calculated by a second index, which included the absolute abundances (A) of all disperser species recorded during the point-counts, respectively, and their relative importance for the seed dispersal (I):

$$D = \sum_{i=1}^{s} (A \times I)$$

The disperser availability values obtained for every point-count were pooled for each ten-day period, and their temporal synchronization with fruit abundance was tested by multiple regression analysis including disperser availability and a time ("seasonality") factor as independent variables.

Results

Population structure and lifetime reproductive strategy

The populations revealed considerable differences (Table 2): south Iberian plants grew up to tall trees, while central European individuals formed bushes or small trees. A strong correlation between stem diameter and absolute age existed in both study sites (south Iberia: $r^2 = 0.89$, $p < 0.001$, $n = 44$; central Europe: $r^2 = 0.96$, $p < 0.001$, $n = 36$). The average growth rate was higher in south Iberia (t-test: $t = 4.7$, $p < 0.001$, $n = 80$). South Iberian trees were on average more than twice older and reached the reproductive stage much later. The percentage of adult and of currently fruiting individuals was higher in central European populations, while south Iberian trees produced considerably larger fruit crops. The mortality was highest in south Iberian subadults, while in central Europe dead trees were mostly adults.

Avian disperser guilds

In south Iberia 524 foraging visits were recorded. Twelve species ate *F. alnus* fruits, of whose 7 acted as seed dispersers, 4 were pure fruit predators, and 1 exceptionally dispersed seeds (Table 3). All but one of them (*Sylvia borin*) bred in the study area. *Erithacus rubecula*, *Sylvia atricapilla* and *Turdus merula* performed virtually the entire seed dispersal (Table 3). They consumed fruits frequently and mainly used *F. alnus* habitats. All species occurred in more or less constant abundances throughout the ripening season (Fig. 1). No species ate *F. alnus* fruits more often than expected by its abundance in the study area ($\chi^2 = 16.9$, DF = 11, $p < 0.2$, n = 1801).

In central Europe 191 foraging visits were recorded. Eight species dispersed seeds and 2 were fruit predators (Table 3). Three disperser guilds could be distinguished on the temporal scale: four migrant *Sylvia* warblers were replaced later in the ripening season by two thrush species (*Turdus philomelos* and *T. iliacus*), while *E. rubecula* and *T. merula* occurred in largely constant abundances throughout the ripening season (Fig. 1).

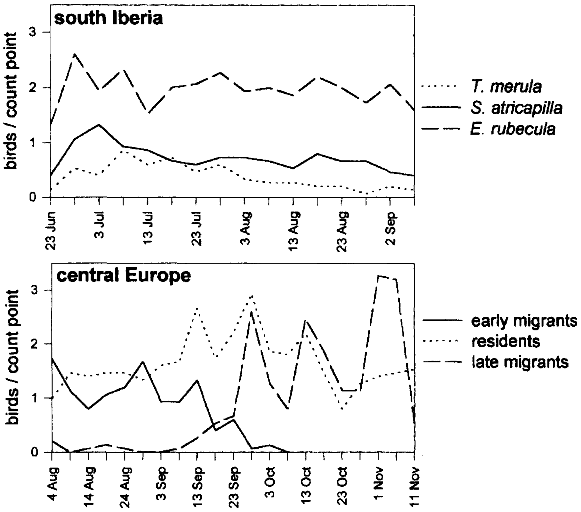

Fig. 1. Abundance of the main dispersers throughout the ripening season in south Iberia and Central Europe; species considered in the central European diagram: early migrants = *Sylvia* spp.; residents = *Turdus merula*, *Erithacus rubecula*; late migrants = *Turdus philomelos*, *Turdus iliacus*.

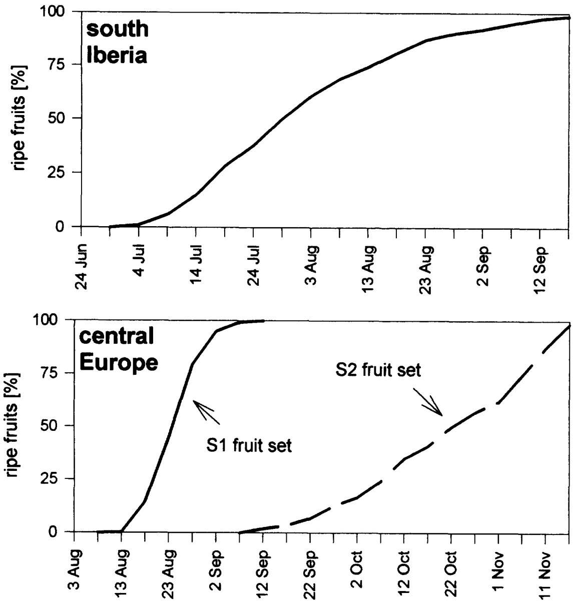

Fig. 2. Ripening phenology of *F. alnus* in south Iberia and central Europe.

Sylvia atricapilla and *S. borin* were the most prominent dispersers (Table 3). Both visited fruiting trees more often than expected by their abundance (*S. atricapilla*: $\chi^2 = 135.7$, $p < 0.001$, *S. borin*: $\chi^2 = 22.7$, $p < 0.001$, n = 1256) and used *F. alnus* habitats more often than other frugivorous species (*S. atricapilla*: $\chi^2 = 72.4$, $p < 0.001$, *S. borin*: $\chi^2 = 8.5$, $p < 0.01$, n = 1256).

Fruit ripening phenology

In south Iberia the fruit ripening season ranged from end of June until mid September. Fruit ripening was asynchronous and resulted in an unimodal distribution of fruit abundance (Fig. 2). In contrast, central European trees produced two sets of fruits that ripened one after the other and were easy to distinguish at the branch level because of the species' acropetal fruit ripening sequence. The first set of fruits (S1, hereafter) matured from the beginning of August until end of September, while the ripening season of the second set (S2) ranged from mid September until November (Fig. 2). Most S2 fruits were abscissed unripe from the marked trees, and the S1 fruit set covered the vast majority (86%) of the total ripe fruit crop.

South Iberian fruits needed less time for maturation (54 ± 2.0 d, n = 27) than central European S1 fruits (69 ± 7.3 d, n = 28) (U-test: $Z = -5.7$, $p < 0.001$, n = 55). None of the marked S2 fruits matured. Fruit maturation both within and among individuals was more synchronized in central European S1 fruits than in central European S2 and south Iberian fruits (Table 4). The ripening synchronization within trees did not differ between Iberian and German S2 fruits, whereas among trees the ripening patterns varied more in south Iberia.

Temporal synchronization of disperser availability and ripening phenology

In south Iberia the overall disperser availability slightly decreased during the ripening season (Fig. 3, $r^2 = 0.68$, $p = 0.01$, n = 8). Multiple regression analyses did not show an effect of disperser availability or seasonality on fruit abundance ($r^2 = 0.25$, $p = 0.48$, n = 8).

In central Europe, the disperser availability changed markedly during the ripening season and was higher during the maturation of the S1 fruit set (Fig. 3, ANCOVA: F = 11.43, $p = 0.01$, covariate seasonality: F = 0.41, $p = 0.54$). The abundance of ripe fruits was correlated with the disperser availability ($r^2 = 0.99$, p =

Table 4. Morphology and chemical composition of south Iberian and central European fruits (S1 and S2 fruit set); mean ± SD, different letters represent significant differences ($p < 0.01$, U-test or χ^2-test).

	south Iberia	central Europe S1	central Europe S2
fruit no. morphometric analyses[1]	200	110	90
fruit length [mm]	8.3 ± 0.6 ^{a}	7.6 ± 0.7 ^{b}	7.6 ± 0.5 ^{b}
fruit diameter [mm]	9.0 ± 0.8 ^{a}	8.2 ± 0.8 ^{b}	8.3 ± 0.6 ^{b}
fruit fresh weight [mg]	403 ± 97 ^{a}	318 ± 86 ^{b}	332 ± 64 ^{b}
seed weight [mg]	37 ± 16 ^{a}	23 ± 12 ^{b}	30 ± 8 ^{c}
seed number	2.9 ± 0.2 ^{a}	2.1 ± 0.3 ^{b}	2.4 ± 0.5 ^{c}
percentage empty seeds	23.3 ^{a}	29.9 ^{b}	9.4 ^{c}
filled seeds per fruit	2.3 ± 0.8 ^{a}	1.5 ± 0.5 ^{b}	2.1 ± 0.6 ^{c}
seed weight per fruit [mg]	111 ± 32 ^{a}	48 ± 15 ^{b}	71 ± 15 ^{c}
pulp/seed ratio	2.7 ± 0.6 ^{a}	5.9 ± 1.3 ^{b}	3.8 ± 1.4 ^{c}
sample no. chemical analyses	10	30	9
water [% fwt]	82.5 ± 1.8 ^{a}	84.5 ± 1.8 ^{b}	86.2 ± 1.4 ^{c}
glucose [% dwt]	25.9 ± 3.1 ^{a}	20.9 ± 3.0 ^{b}	15.2 ± 2.1 ^{c}
fructose [% dwt]	25.8 ± 3.4 ^{a}	26.8 ± 3.5 ^{a}	22.0 ± 2.9 ^{b}
proteins [% dwt][2]	4.3 ± 0.6 ^{a}	5.8 ± 1.2 ^{b}	8.9 ± 1.1 ^{c}
ash [% dwt]	4.0 ± 0.3 ^{a}	3.0 ± 0.5 ^{b}	3.2 ± 0.3 ^{b}
lipids [% dwt]	2.4 ± 0.7 ^{a}	2.8 ± 1.0 ^{a}	2.7 ± 0.8 ^{a}
phenolic compounds [% dwt]	2.3 ± 0.5 ^{a}	1.8 ± 0.1 ^{b}	1.8 ± 0.1 ^{b}
metabolizable energy content per fruit [kJ][3]	0.54 ± 0.11 ^{a}	0.44 ± 0.13 ^{b}	0.33 ± 0.08 ^{c}

[1] 20 fruits per south Iberian and 10 fruits per central European individual, respectively.
[2] calculated by total nitrogen content multiplicated with 6.25.
[3] calculated by the caloric values of summed soluble carbohydrates, lipids and proteins.

0.01, n = 10) but not with seasonality ($r^2 = 0.24$, p = 0.45, n = 10).

Fruit traits

Despite high individual variation, south Iberian and central European fruits showed significant differences in most of the measured traits (Table 5). South Iberian fruits were bigger and contained both more and bigger seeds per fruit than central European fruits, which lead to a considerably lower pulp/seed ratio. Most chemical constituents also differed significantly.

Central European S1 and S2 fruits showed some differences, too: seed number, seed mass and percentage of filled (i.e. putatively viable) seeds were higher in S2 fruits. Less seed load and higher contents in soluble carbohydrates resulted in a considerably higher pulp/seed ratio and energy content per fruit in S1 than in S2 fruits.

Discussion

Differentiation of the lifetime reproductive strategy

Our results show that the studied *F. alnus* populations have undergone an extense process of phenotypic differentiation. The central European populations bear a phenotype with a considerably shortened generation turnover compared to the south Iberian type. The diminished plants begin soon to produce fruits, while the tall south Iberian trees pass a long stage of establishment and elevated mortality within the mature forest vegetation before they start to reproduce. Theoretically, a central European *F. alnus* genet can propagate four times until a south Iberian individual arrives to produce propagules for the first time. In turn, established south Iberian trees have a life expectancy of 60–65 yr while central European trees reach scarcely > 30–35 yr. According to Grime's (1977) ordination of primary plant strategies, the south Iberian *F. alnus* populations rather show a competitive strategy with

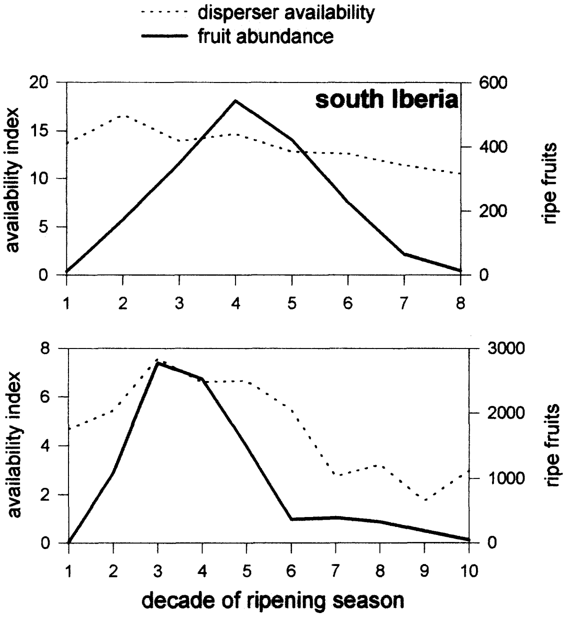

Fig. 3. Temporal synchronization of disperser availability and fruit abundance in south Iberia and central Europe.

Table 5. Relative importance (I) of species eating *F. alnus* fruits. Frugivory: SD = seed disperser, SP = seed predator, PP = pulp predator (sensu Jordano 1992). + = recorded in the study area but no foraging records, – = not recorded in the study area.

species	frugivory	$I_{\text{south Iberia}}$	$I_{\text{central Europe}}$
Dendrocopus major	SP	<0.001	+
Erithacus rubecula	SD	0.291	0.057
Fringilla coelebs	SP	<0.001	+
Garrulus glandarius	SD	0.002	+
Muscicapa striata	SD	0.002	–
Parus caeruleus	PP (SD)[1]	0.133	+
Parus major	PP	<0.001	0.001
Pyrrhula pyrrhula	SP	–	0.038
Sitta europaea	SP	<0.001	+
Sylvia atricapilla	SD	0.24	0.431
Sylvia borin	SD	0.003	0.211
Sylvia communis	SD	–	0.048
Sylvia curruca	SD	–	0.003
Turdus iliacus	SD	–	0.067
Turdus merula	SD	0.325	0.067
Turdus philomelos	SD	–	0.077
Turdus viscivorus	SD	<0.001	–
Σ		1.0	1.0

[1] exceptionally dispersing seeds by carrying entire fruits away.

strong vegetative growth prior to reproduction and a long life expectancy, while the phenotype of the central European populations exhibits characteristics of a rather ruderal species, characterized by colonization of early-successional habitats, small size, early and regular fruiting, and a short lifespan.

The disperser guilds

The characters of the compared disperser guilds vary although several bird species are involved in both study areas. In south Iberia almost the entire dispersal of *F. alnus* seeds is realized by three small- to medium-sized species (*Erithacus rubecula*, *Sylvia atricapilla* and *Turdus merula*), which share a comparable importance. All are residents and occur in more or less constant abundances throughout the ripening season. Contrastingly, in central Europe the entire seed dispersal is carried out by migrating birds, which are more mobile during foraging than residents (Berthold 1993). According to the migration phenology, the disperser availability changes considerably throughout the ripening season. The most important dispersers, *Sylvia atricapilla* and *S. borin*, occur only during the early ripening season. Both provide the highest quantity and quality of seed dispersal, and their importance suggests mainly to be limited by their restricted presence in the area. Interestingly, both species frequent scrublands during migration, whereas during the breeding season they prefer more woody habitats (Cody 1978, Bairlein 1981, Carbonell and Tellería 1998). The prevalence of fleshy-fruited plant species in central European scrublands (Kollmann 1997) and the resulting high fruit availability may be one reason for the habitat shift of these species, that show strong frugivory during migration (Brensing 1977, Bairlein and Gwinner 1994). Other disperser species which are present during the late or the whole ripening season lack comparable importance, although some of them are considerably longer present than the *Sylvia* warblers.

Differentiation of dispersal traits

The considerable differences in ripening phenology and fruit design of *F. alnus* may in part be interpreted as adaptions to their respective disperser guilds, although we cannot quantify the influence of environmental or developmental constraints, which may play a more or less important role in shaping the studied traits (Primack 1987, Eriksson and Ehrlén 1991, 1998, Herrera 1995). Other studies on intraspecific geographical variation of fruiting phenology (Fuentes 1992, Guitián 1998) found that adaptive adjustments to disperser availability were counteracted by climatic constraints on fruit development. Our study areas undergo largely different climatic conditions: while in the fruiting period of south Iberian populations is mainly limited by drought in late summer, central European trees have to complete their entire growth, flowering and fruiting between April and October/November. The respective utilization of breeding and migrant disperser guilds at the two study sites integrates and "neutralizes" these climatic constraints and thus facilitates a divergent fine-scale synchronization between fruit abundance and disperser availability: the asynchronous ripening sequence of south Iberian *F. alnus* populations coincides with a constant availability of seed dispersers throughout the ripening season. Successively maturing fruit crops provide a predictable long-term food source for resident birds (Snow and Snow 1988, Smith and Riley 1990), and in turn the risk of disperser satiation is minimized (Jordano 1987, 1995c). Contrastingly, in central Europe the predictable and concentrated autumn passage of the most important dispersers, *Sylvia atricapilla* and *S. borin*, coincides with a massive abundance of fruits, which is caused by a strong intra- and interindividual synchronization of the S1 fruit set (see also Kollmann and Pirl 1995). On the other hand, the asynchronous fruit ripening sequence of the S2 fruit set is correlated with the less predictable long-term occurrence of migrating and wintering nomadic thrush flocks. Several studies have shown that ripening patterns of different species within temperate plant communities may vary in correlation with temporal regularity and abundance of their respective dispersers (Thompson and Willson 1979, Stapanian 1982, Piper 1986, Skeate 1987, Eriksson and Ehrlén 1991). But up to our knowledge no study has explicitly revealed a differentiated ripening pattern neither between different populations of the same species nor even within one ripening season of the same population.

The switch between resident and migrant dispersers and the resulting shift of their relative importance suggest that selective patterns on the fruit design have also changed (Jordano 1995c). Selection by frugivores on the individual fruit level has mostly been shown to depend on fruit size and seed load (Herrera 1981, Snow and Snow 1988, Jordano 1992, 1995a, Sallabanks 1993b, Alcántara et al. 1997). In our study both traits exhibit considerable differences, which coincide with adaptionistic expectations: the small-sized *Sylvia* warblers should select for small fruits with few, small seeds, which were found in the central European S1 fruit set. The costs of this fruit design – less nutrient reserves per seed and a reduced number of seeds dispersed per fruit – may be a contribution to high competition for seed dispersers (Herrera 1981, Kollmann and Pirl 1995). Nevertheless, the intermediate seed size and number of central European S2 fruits also suggest that external factors additionally influence these traits. At most differences in the chemical fruit composition we also cannot evidently distinguish adaptive functions from environmental factors (e.g. nutrient availability or weather conditions, Chiarucci et al. 1993). Nevertheless, the reduced and quite invariable content of phenolic substances in central European fruits cannot easily be explained by environmental conditions and may be an adaptation to reduce deterrent effects on the main dispersers, which are highly frugivorous during migration (Brensing 1977, Bairlein and Gwinner 1994, Bairlein 1996). A selection on phenolic compound contents by herbivore pressure (Cipollini and Levey 1997) may be neglected since both herbivory by cervids and fruit infestation by insects were considerably stronger in central Europe (Hampe unpubl.). Furthermore, a comparison between the central European S1 and S2 fruit set reveals decreasing soluble carbohydrate and increasing nitrogen contents, which was hypothesized by Stapanian (1982) to outweigh the availability of protein-rich insect food. Additionally, high contents of easily metabolizable carbohydrates enhance frugivorous migrant warblers to maintain high energy intake rates (Fuentes 1994, Bairlein and Gwinner 1994). Nevertheless, Eriksson and Ehrlén (1991, 1998) found no supporting or even opposite trends. An alternative, nonadaptive explanation for our results may be that the late ripening S2 fruits receive additional nitrogen resorbed from senescent leaves, while the reduced content of soluble carbohydrates is due to a diminished photosynthetic capacity (Pakonen et al. 1988, Aerts 1996).

Central European *F. alnus* trees tend to show a dispersal syndrome adjusted to their uniform main disperser guild (small-sized migrant *Sylvia* warblers), which provides an intense and high quality seed dispersal but sets narrower limits on both ripening phenology and fruit design than the south Iberian guild. The measured differences suggest that divergent abundance patterns and preferences of changing disperser guilds may induce adaptive adjustments of plant dispersal traits on larger time scales, although selection on fruit design by frugivores is usually weak and overwhelmed by effects of plant fecundity (Jordano 1987, 1995a, Sallabanks 1993b, Alcántara et al. 1997). Thus, our results support the assertation of Willson and Whelan (1993) and Jordano (1995c) that even small changes in the qualitative character of disperser guilds, which are not recognized during short-term ecological studies, may play an important role in shaping dispersal traits on time scales of several thousands of years.

Conclusions

The studied *F. alnus* populations have undergone considerable phenotypic differentiations since their genetic isolation. Compared to the relict populations in south Iberia, the following differentiations support an increased propagation potential within the populations of the central European *F. alnus* phenotype: 1) a highly accelerated generation turnover, 2) the utilization of migrating birds as dispersers, and 3) a fine-scale adjustment of dispersal traits to a guild of high quality seed dispersers. We cannot quantify the influence of environmental conditions on the studied traits, but the degree of differentiation strongly suggests that differences are not only due to phenotypic plasticity (West-Eberhard 1989) but possess a genetic basis and therefore are a result of microevolutionary processes (see Thompson 1994). Why and when did *F. alnus* experiment these differentiations? We suggest that their origin was promoted by the rapidly changing environmental conditions during the transitions between glacial and interglacial periods, which caused a spatial separation of phenotypes with different propagation capacities and a subsequent disruptive selection (Huntley and Webb 1989, see also Wade and Goodnight 1998). Quickly rising temperatures opened large regions of low competition for populations that rapidly advanced from the northern edges of the glacial refugia (Bennett and Lamb 1988, Hewitt 1996), while the increasing summer drought in the Mediterranean basin forced southern populations to regret into habitats with particular microclimates like the south Iberian gallery forests, which are characterized by a high competivity of the dominant species. The rapid migration process itself presumably further supported the development of a short-lived, mobile "colonizer" phenotype within the northward advancing populations (Bennett 1986, Brubaker 1986, Clark 1998). In contrast, the geographical distribution of the south Iberian *F. alnus* probably shifted vertically rather than horizontally during transitions between glacial and interglacial periods (Bennett et al. 1991, Vogel et al. 1999), and the absolute distances covered by the migrating populations were much smaller than these covered by their northern conspecifics. Therefore it may be assumed that selection on genet mobility was less pronounced in the Iberian populations while selection on competitive capacity was higher (Hampe and Bairlein 1999b).

The current amount of difference suggests that the compared populations may even represent different species rather than subspecies. Future genetic analyses of several populations along a south-north gradient (Hampe and Arroyo unpubl.) may reveal their taxonomic status and simultaneously elucidate the time frame of the differentiation process. It seems reasonable to assume that the current differences accumulated over several transitions between Quaternary glacial and interglacial periods (Suc 1984, Hewitt 1996). Other studies on tree species (Cwynar and MacDonald 1987, Lagercrantz and Ryman 1990) could date intraspecific morphological differentiations to the Holocene period, but these were less pronounced than the differences found in the present study. Our hypothesis that the recent degree of differentiation accumulated over time is furthermore supported by the observation that only *F. alnus* plants of northern Anatolia and the Caucasus – another region well-known for its rich Tertiary relict flora – show the same treelike habit of *F. alnus baetica* (Ern pers. comm.), while up to our knowledge all the rest of the distribution area is uniformly covered by shrublike phenotypes.

Independent of the exact time frame *F. alnus* needed to develop its current degree of variability, our results support Charles-Dominique's (1993) hypothesis that the recent diversity of zoochorous dispersal traits have evolved in short stages of intense diversification changing with long stages of stability. Finally, our results underline once more the significance of glacial relict populations for the long-term conservation of the genetic and phenotypic diversity of the European tree flora (see Broyles 1998, Newton et al. 1999 and references therein).

Acknowledgements – We thank Javier Sánchez for the permission to work in the "Los Alcornocales" nature reserve and his support in the area. Juan Arroyo offered varied valuable support on the study. Ralph Boetz and Melanie Massaro helped with the field work. Helpful advices of Pedro Jordano and discussions with Kjell Bolmgren improved the study. Hartmut Ern showed us "his" treelike alder buckthorns from Anatolia and Georgia. The study was supported by an ERASMUS grant of the European Union to A.H, the Deutsche Ornithologen-Gesellschaft and the DGICYT grant PB95-0551 (Juan Arroyo).

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