

Table 1. Taxonomic and phylogenetic diversity components across Europe

Level	Diversity		
	γ	β	α
Taxonomic level			
Original flora	10,928	0.5432 \pm 0.1622	2,194 \pm 1194
Current total flora	12,624	0.5155 \pm 0.1490	2,664 \pm 1215
Phylogenetic level			
Original flora	1.3797	1.4493 \pm 0.1049	1.4772 \pm 0.0202
Current total flora	1.3942	1.4462 \pm 0.0951	1.4725 \pm 0.0189

γ applies to overall European diversity, whereas β and α are mean values (\pm SD) across European regions. Taxonomic diversities are based on species numbers (γ and α) and β_{tax} values. Phylogenetic diversities are based on Δ^+ (γ and α) and β_{phyl} values.

(phylogenetic overdispersion) (36) or (ii) more closely related species (phylogenetic clustering) (37; and see ref. 38 for review).

Generally, very little is known about the relative effects of extinctions and invasions on phylogenetic relationships among species at large spatial scales (27). On the basis of a comprehensive dataset of original (before extinctions and introductions) and current (after extinctions and introductions) floras across several European regions, here we use phylogenetic information to assess the consequences of species extinctions and introductions on taxonomic and phylogenetic diversity.

Results and Discussion

Since AD 1500, the processes of species extinctions and invasions, acting in concert, resulted in a net increase in overall European plant species richness (γ -diversity) (Table 1). This increase is due to 69 extinctions of European plants and 1,621 invasions of plants from outside Europe (Fig. S1 and Table S1) and is also accompanied by increased phylogenetic γ -diversity. The increased species richness at the European level is reflected by higher species richness in all European regions (α -diversity), where species invasions also exceeded extinctions (Table S1). However, the prevalence of invasions over extinctions decreased rather than increased phylogenetic α -diversity over the same period; an additional decrease was caused by extinctions (both $P < 0.001$; Table 1, Table S1, and Table S2).

Despite increased species richness at the European and regional level, extinctions and invasions in concert resulted in decreased β -diversity among species (β_{tax}) and β -diversity among phylogenetic lineages (β_{phyl}) of European regions (Table 1), indicating that European floras became phylogenetically and taxonomically impoverished. A decrease of phylogenetic richness with increasing species richness was previously reported on a national scale (39).

However, considering extinctions and invasions separately revealed contrasting patterns. Invasions have generally led to taxonomic and phylogenetic homogenization, whereas species extinctions result in differentiation. Species extinctions increased β_{tax} and β_{phyl} (Fig. 1B), although β_{tax} and β_{phyl} of extinct species were higher than those of extant native species ($P < 0.001$). Species from distantly related taxonomic branches have become extinct in different regions. By contrast, invasions decreased β_{tax} and β_{phyl} of European floras (Fig. 1C), although β_{tax} and β_{phyl} of alien species was higher than those of native species (both $P < 0.001$). Hence, although alien floras are taxonomically and phylogenetically diverse, the constituent species are either native to other European regions or, if introduced from outside Europe, tend to be closely related to native European species.

We reason that many species that have become extinct or have been introduced in a particular region are components of the current native floras of other European regions, because (i) the loss of taxonomically more diverse native species (extinctions) led to increased β_{tax} , and the gain of more diverse aliens led to

decreased β_{tax} ; and (ii) invasions of phylogenetically more diverse alien species decreased β_{phyl} , and the loss of more diverse extinct species increased β_{phyl} among floras. This is because extinctions of plant species in Europe are mainly regional rather than continent-wide extinctions. Moreover, ca. 53% of plant invasions in European floras are due to species exchange among European regions (40). Such a high percentage is likely to increase taxonomic and phylogenetic similarities among European floras.

Generally, the negative effect of aliens on β_{tax} and β_{phyl} is approximately seven times the magnitude of the positive effect of species losses (compare β_{tax} values, Fig. 1B and C). Therefore, the taxonomic and phylogenetic homogenization among European floras due to species invasions masks any regional differentiation due to species extinctions. These patterns are consistent with those found for North America, where species extinctions only played a minor role in defining compositional patterns for state floras, owing to the low numbers of extinct species (41). Although extinction processes are much slower than invasions, it is unlikely that accounting for lag effects in extinctions (8) would change the pattern dramatically.

With compositional changes due to extinctions and invasions, β_{tax} increased linearly with increasing β_{phyl} (Fig. 1A; $R^2 = 0.86$, $P < 0.001$). However, this relationship is not inevitable (27); the high correlation indicates that species determining this pattern are probably widespread and closely related to extant native species. The weaker relationship between β_{tax} and β_{phyl} derived from the effect of extinctions indicates that there were more phylogenetically unique species among extinct native plants. In contrast to the main patterns, among some regions we did observe occasions when species introductions led to taxonomic and phylogenetic differentiation, and in some circumstances extinctions led to increased homogenization (as species that are unique to only one region are lost). However, we did not find any systematic trend in these patterns, and they were not related to geographic distance, species richness, or other specific attributes of the floras (e.g., level of endemism).

As with α -diversity, two scenarios whereby β_{tax} and β_{phyl} show contrasting patterns (homogenization vs. differentiation) are possible (27): (i) a high β_{tax} (differentiation) and a low β_{phyl} (homogenization) could be observed with a high proportion of resident endemic species or if the different communities consist of close congeners; (ii) a low β_{tax} (homogenization) and a high β_{phyl} (differentiation) is very unlikely, because a high species overlap will always generate a high phylogenetic overlap (27).

Effects of scale dependencies are known for biodiversity patterns in general (42) and invasion processes in particular (43, 44). Phylogenetic structures could also be scale dependent (45). It has been argued that large-scale patterns of phylogenetic clustering reflect biogeographic rather than ecologic processes (38). Moreover, the perception of taxonomic homogenization is dependent on the spatial scale at which samples are gathered and

assigned to different categories in different regions [e.g., 1,726 species are native to one region but are alien to another (see ref. 40), or 468 native species are extinct in one region but occur in other regions (Table S1).

Taxonomic β -Diversity. We used the Morisita-Horn dissimilarity index (MH) to calculate β_{tax} among floras. The index is computed as:

$$\beta_{\text{tax}} = \text{MH}_{jk} = 1 - \frac{2 \sum_i (x_{ij}x_{ik})}{(\lambda_j + \lambda_k) \sum_i x_{ij} \sum_i x_{ik}},$$

$$\text{with } \lambda_j = \frac{\sum_i x_{ij}^2}{\left(\sum_i x_{ij}\right)^2} \text{ and } \lambda_k = \frac{\sum_i x_{ik}^2}{\left(\sum_i x_{ik}\right)^2},$$

where x_{ij} and x_{ik} represent the frequency of species i in regions j and k , respectively. The index ranges from 0 (total identity between two samples and low β -diversity) to 1 (absolute dissimilarity of these samples and high β -diversity). This index is less sensitive to species richness and sample size than most other indices (59). Because the index needs abundance data, we defined pseudo-abundance of one for each species.

Phylogenetic β -Diversity. β_{phy} was defined as β -diversity with a temporal dimension measured as phylogenetic distance between communities according to branch lengths (27). The online software tool *Phylomatic* (60) was used to construct a supertree using species and genus data of all species considered. In the absence of phylogenetic branch lengths for the whole tree, we calculated pseudobranch lengths to weight the height of the nodes according to their position in the tree (61). We assigned a relative height (with tips at 0 and root at 1) to each node and then calculated branch lengths as the difference between the heights of two nodes. This ensures that the total branch length from root to any tip is constant. Grafen's method sets node height from the tip proportional to the number of descendent terminal nodes (taxa) minus 1 (61). To calculate the branch length we used the function *brlen* of the R-package *ape* (62).

The β_{phy} between two floras was assessed using the *PhyloSor* index (37). To facilitate the comparison of β_{phy} and β_{tax} , β_{phy} was also computed as dissimilarity:

$$\beta_{\text{phy}} = 1 - \text{PhyloSor}_{jk}, \text{ with } \text{PhyloSor}_{jk} = \frac{BL_{jk}}{(BL_j + BL_k) \frac{1}{2}}.$$

BL_{jk} is the branch length common to communities j and k , and BL_j and BL_k are the total branch lengths of community j and k , respectively. β_{phy} ranges from 0 (both communities are composed of the same taxa) to 1 (two communities share no taxa).

To disentangle the effect of the loss and gain of species on the β -diversity between regions at the species (β_{tax}) and phylogenetic (β_{phy}) level, we separated the processes of species extinctions and invasions. Because comprehensive dates of plant extinctions do not exist, we arbitrarily defined that all extinctions occurred after AD 1500. Thus, we defined the "original flora" (before AD 1500) as all extant and extinct native species, the "current native flora" as only extant native species, and the "current total flora" as extant natives and alien species. Introducing these three categories, we calculate different effects of different floristic elements on β_{tax} and β_{phy} : (i) the combined effect as the difference between the β -diversities of original and current flora [$\beta_{\text{(current total flora)}} - \beta_{\text{(original flora)}}$]; (ii) the effect of extinct native species as the difference between β -diversities of original and current native flora [$\beta_{\text{(current native flora)}} - \beta_{\text{(original flora)}}$]; and (iii) the effect of alien species as the difference between β -diversities of current total flora and current native flora [$\beta_{\text{(current total flora)}} - \beta_{\text{(current native flora)}}$]. Furthermore, we calculated separately the β_{tax} and β_{phy} of extinct, alien, and native species among regions.

Alpha Diversity. Beside taxonomic α -diversity in terms of species numbers (Table S2), we also assessed phylogenetic α -diversity of the original and current floras by using Warwick's average taxonomic distinctness (Δ^+) (63). Δ^+ was originally developed on taxonomic relationships but can be adapted to phylogenetic information (64). The index was calculated as:

$$\Delta^+ = \frac{\sum Br_i}{s^*(s-1)},$$

where Br_i is built from the distance matrix of species based on branch lengths, and s is the number of species. The index is based on the sum of branch lengths between species (as provided by the distance matrix) and can be interpreted as the mean distance between two randomly chosen species independent of their distance from the root of the tree. Δ^+ is mathematically unbiased by species richness; that is, it does not automatically increase with sample size and reflects the phylogenetic structure of a subset from a phylogenetic tree best, unlike the majority of other available phylogenetic diversity indices (64). Smaller Δ^+ values indicate that, on average, the assemblage of species is phylogenetically more closely related and less distinct. Analogous to β_{tax} and β_{phy} , we calculated (i) combined effect [$\Delta^+_{\text{(current total flora)}} - \Delta^+_{\text{(original flora)}}$], (ii) extinct effect [$\Delta^+_{\text{(current native flora)}} - \Delta^+_{\text{(original flora)}}$], and (iii) alien effect [$\Delta^+_{\text{(current total flora)}} - \Delta^+_{\text{(current native flora)}}$]. Significant differences between all relationships of β -diversity or Δ^+ were assessed using Fisher's paired comparisons design test (65).

ACKNOWLEDGMENTS. We thank Stefan Michalski and Emmanuel Paradis for providing phylogenetic and technical expertise; and the Delivering Alien Invasive Species Inventories for Europe (DAISIE) consortium for providing the data. This study was partly funded by the European Union through the FP 6 projects DAISIE (contract number SSPI-CT-2003-511202) and ALARM (GOCE-CT-2003-506675). M.H., J.P., and P.P. were also supported by Grants AV0260050516 (from the Academy of Sciences of the Czech Republic), MSM0021620828, and LC06073 (both from the Ministry of Education, Youth and Sports of the Czech Republic).

- Elton CS (1958) *The Ecology of Invasions by Animals and Plants* (Methuen, London).
- Davis MA (2003) Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience* 53:481-489.
- Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J Appl Ecol* 46:10-18.
- Pyšek P, et al. (2004) Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53:131-143.
- Sax DF, Gaines SD (2003) Species diversity: From global decreases to local increases. *Trends Ecol Evol* 18:561-566.
- Hobbs RJ, Mooney HA (1998) Broadening the extinction debate: Population deletions and additions in California and Western Australia. *Conserv Biol* 12:271-283.
- Stohlgren TJ, Barnett DT, Jarnevich CS, Flather C, Kartesz J (2008) The myth of plant species saturation. *Ecol Lett* 11:313-322.
- Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. *Am Nat* 160:766-783.
- Wilson K-J (1997) Extinct and introduced vertebrate species in New Zealand: A loss of biodiversity and gain in biodiversity. *Pac Conserv Biol* 3:301-305.
- Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *Am Nat* 162:442-460.
- Cassey P, Blackburn TM, Lockwood JL, Sax DF (2006) A stochastic model for integrating changes in species richness and community similarity across spatial scales. *Oikos* 115:207-218.

- McKinney ML (2005) Species introduced from nearby sources have a more homogenizing effect than species from distant sources: Evidence from plants and fishes in the USA. *Divers Distrib* 11:367-374.
- Winter M, Kühn I, Nentwig W, Klotz S (2008) Spatial aspects of trait homogenization within the German flora. *J Biogeogr* 35:2289-2297.
- Rahel FJ (2002) Homogenization of freshwater faunas. *Annu Rev Ecol Syst* 33:291-315.
- Olden JD, Poff NL, McKinney ML (2006) Forecasting faunal and floral homogenization associated with human population geography in North America. *Biol Conserv* 127:261-271.
- Spear D, Chown SL (2008) Taxonomic homogenization in ungulates: Patterns and mechanisms at local and global scales. *J Biogeogr* 35:1962-1975.
- McKinney ML (2002) Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Glob Ecol Biogeogr* 11:343-348.
- Duncan JR, Lockwood JL (2001) in *Biotic Homogenization*, eds McKinney ML, Lockwood JL (Kluwer Academic/Plenum, New York), pp 247-256.
- Marchetti MP, et al. (2001) in *Biotic Homogenization*, eds Lockwood JL, McKinney ML (Kluwer Academic/Plenum Publishers, New York), pp 259-278.
- Castro SA, Jaksic FM (2008) How general are global trends in biotic homogenization? Floristic tracking in Chile, South America. *Glob Ecol Biogeogr* 17:524-531.
- Rooney TP, Wiegmann SM, Rogers DA, Waller DM (2004) Biotic impoverishment and homogenization in unfragmented forest understorey communities. *Conserv Biol* 18:787-798.
- Vane-Wright RI, Humphries CJ, Williams PH (1991) What to protect?—Systematics and the agony of choice. *Biol Conserv* 55:235.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475-505.

24. Maherali H, Klironomos JN (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316:1746–1748.
25. Jump AS, Marchant R, Penuelas J (2009) Environmental change and the option value of genetic diversity. *Trends Plants Sci* 14:51–58.
26. Chave J, Chust G, Thébaud C (2007) in *Scaling Biodiversity*, eds Storch D, Marquet P, Brown JH (Cambridge Univ Press, Cambridge, UK), pp 151–167.
27. Graham CH, Fine PVA (2008) Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecol Lett* 11:1265–1277.
28. Vamasi JC, Wilson JR (2008) Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecol Lett* 11:1047–1053.
29. Pyšek P, Richardson D (2007) in *Biological Invasions, Ecological Studies*, ed Nentwig W (Springer, Berlin), Vol 193, pp 97–126.
30. Freville H, McConway K, Dodd M, Silvertown J (2007) Prediction of extinction in plants: Interaction of extrinsic threats and life history traits. *Ecology* 88:2662–2672.
31. Gaston KJ (1998) Species-range size distributions: Products of speciation, extinction and transformation. *Philos Trans R Soc Lond B Biol Sci* 353:219–230.
32. Sechrest W, et al. (2002) Hotspots and the conservation of evolutionary history. *Proc Natl Acad Sci USA* 99:2067–2071.
33. Mace GM, Gittleman JL, Purvis A (2003) Preserving the tree of life. *Science* 300:1707–1709.
34. Pyšek P, et al. (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Divers Distrib* 15:891–903.
35. Pyšek P (1998) Is there a taxonomic pattern to plant invasions? *Oikos* 82:282–294.
36. Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA (2004) Phylogenetic overdispersion in Floridian oak communities. *Am Nat* 163:823–843.
37. Bryant JA, et al. (2008) Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. *Proc Natl Acad Sci USA* 105:11505–11511.
38. Proches S, Wilson JR, Richardson DM, Rejmanek M (2008) Searching for phylogenetic pattern in biological invasions. *Glob Ecol Biogeogr* 17:5–10.
39. Knapp S, Kühn I, Schweiger O, Klotz S (2008) Challenging urban species diversity: Contrasting phylogenetic patterns across plant functional groups in Germany. *Ecol Lett* 11:1054–1064.
40. Lambdon PW, et al. (2008) Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80:101–149.
41. Qian H, Ricklefs RE (2006) The role of exotic species in homogenizing the North American flora. *Ecol Lett* 9:1293–1298.
42. Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: Towards a general, hierarchical theory of species diversity. *J Biogeogr* 28:453–470.
43. Rouget M, Richardson DM (2003) in *Plant Invasions: Ecological Threats and Management Solutions*, eds Child LE, et al. (Backhuys, Leiden), pp 3–15.
44. Kühn I, Klotz S (2007) in *Biological Invasions, Ecological Studies*, ed Nentwig W (Springer, Berlin), Vol 193, pp 181–196.
45. Cavender-Bares J, Keen A, Miles B (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:5109–5122.
46. Hulme PE (2008) Contrasting alien and native plant species-area relationships: The importance of spatial grain and extent. *Glob Ecol Biogeogr* 17:641–647.
47. Lambdon PW, Hulme PE (2006) How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. *J Biogeogr* 33:1116–1125.
48. Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecol Lett* 11:674–681.
49. Olden JD (2006) Biotic homogenization: A new research agenda for conservation biogeography. *J Biogeogr* 33:2027–2039.
50. Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474.
51. Hulme PE (2007) in *Biodiversity Under Threat, Issues in Environmental Science and Technology*, eds Hester R, Harrison RM (Royal Society of Chemistry, Cambridge, UK), pp 56–80.
52. Sax DF, Gaines SD (2008) Species invasions and extinction: The future of native biodiversity on islands. *Proc Natl Acad Sci USA* 105:11490–11497.
53. McKinney ML, Lockwood JL (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14:450–453.
54. Purvis A, Hector A (2000) Getting the measure of biodiversity. *Nature* 405:212–219.
55. Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol Evol* 23:619–630.
56. Hulme PE, Pyšek P, Nentwig W, Vila M (2009) Will threat of biological invasions unite the European Union? *Science* 324:40–41.
57. Tutin TG, et al. (1964–1980) *Flora Europaea* (Cambridge Univ Press, Cambridge, UK).
58. DAISIE (2009) *Handbook of Alien Species in Europe* (Springer, Dordrecht).
59. Wolda H (1981) Similarity indexes, sample-size and diversity. *Oecologia* 50:296–302.
60. Webb CO, Donoghue MJ (2005) Phylomatic: Tree assembly for applied phylogenetics. *Mol Ecol Notes* 5:181–183.
61. Grafen A (1989) The phylogenetic regression. *Philos Trans R Soc Lond B Biol Sci* 326:119–157.
62. Paradis E, Claude J, Strimmer K (2004) APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* 20:289–290.
63. Warwick RM, Clarke KR (1998) Taxonomic distinctness and environmental assessment. *J Appl Ecol* 35:532–543.
64. Schweiger S, Klotz S, Durka W, Kühn I (2008) A comparative test of phylogenetic diversity indices. *Oecologia* 157:485–495.
65. Manly BFJ (1991) *Randomization and Monte Carlo Methods in Biology* (Chapman & Hall, London).