Colonization of high altitudes by alien plants over the last two centuries

Petr Pyšek[a,b,1], Vojtěch Jarošík[a,b], Jan Pergl[a], and Jan Wild[a]

[a]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic; and* [b]*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 01 Prague, Czech Republic*

The paper by Alexander et al. (1) provides an elegant explanation for global patterns of alien species richness in mountain regions. These authors conclude that evolutionary factors such as differential rates of speciation may be less relevant for explaining the patterns of alien species richness than dispersal processes or preadaptation of species to abiotic and biotic conditions (1). One of the important conclusions of their study is that the decrease in alien species richness with increasing altitude is caused by a progressive loss of species, and therefore, the species found at high altitudes are those with the widest ranges that also occurred at low elevations. This implies that gradual spread of alien species after their introduction was a major process involved in shaping the currently observed patterns. This contention raises the issue of the dynamics of these processes over time: have these remained constant or changed? Although robust evidence has accumulated in the literature that plant invasions into high altitudes are limited compared with lower altitudes (2–8), it has yet to be adequately shown whether the colonization of high altitudes by alien plants is a stochastic process of spread in time or if changing conditions in high altitudes have made this environment more favorable to plant invasions.

Existing data on the distribution of alien plants in the Czech Republic, Central Europe (9), provide insights into these processes on a regional geographical scale of 78,000 km^2 (with an altitudinal range of 117–1,602 m above sea level resulting in a steep climatic gradient of *ca*. 10 °C) and time scale of centuries. For 65 alien species (species list in ref. 10) introduced to this country after A.D. 1500 and now naturalized (forming self-reproducing populations in the wild) (11), there are 28,288 dated records of occurrence (localities) starting in 1738. Such data make it possible to determine for each species (*i*) the year of the first record, hence its minimum residence time expressed as the time elapsed since its introduction to the country (12), (*ii*) altitude of its first recorded locality in the region, and (*iii*) current altitudinal range (minimum and maximum). They reveal that alien species gradually penetrated into higher altitudes and that this process occurred not only as a consequence of physical spread but also because it was becoming increasingly easier to colonize such areas.

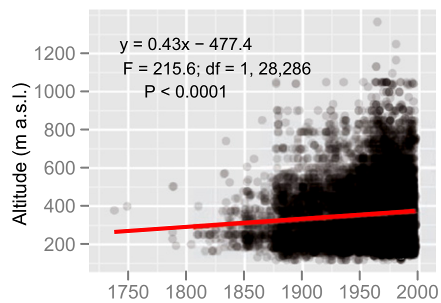

Fig. 1. Altitude of individual records of alien plants in the Czech Republic regressed on the year of the record. An alternative model with the identity of individual species included was also highly significant ($F = 52.0$; df = 129, 28,158; $P < 0.001$) and showed that the pattern of colonization of higher altitudes was species-specific (deletion test on the differences in regression slope of the individual species on the year of the record: $F = 7.49$; df = 64, 28,223; $P < 0.001$).

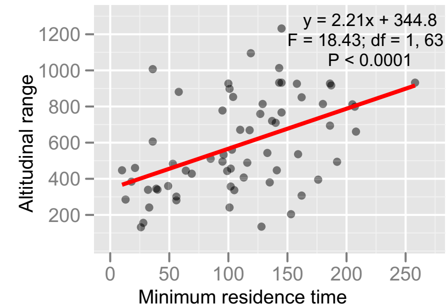

Fig. 2. Altitudinal range of 65 species of neophytes regressed on their minimum residence time (i.e., time since their first record in the Czech Republic).

That, over the last two and a half centuries, alien species gradually colonized increasingly higher altitudes is obvious from a highly significant increase in the altitude of localities at which alien species were being recorded (Fig. 1). Consequently, their altitudinal ranges were increasing over time, as illustrated by a highly significant relationship between a species altitudinal range and minimum residence time; species introduced earlier have larger altitudinal ranges than those introduced more recently (Fig. 2), which is because of the fact that time is needed for either dispersal or genetic adaptation (1).

Alexander et al. (1) suggest that most alien plant species first arrive at low altitudes, where anthropogenic propagule pressure is greatest, and spread upward from there, either naturally or through human agency. In fact, alien plants in the Czech Republic spread in both directions, both to lower and higher altitudes. On average, species were introduced to 310 ± 78 m a.s.l. (mean ± SD, $n = 65$), but their current altitudinal minima and maxima are 142 ± 18 and 731 ± 261 m a.s.l., respectively. However, only upward spread was contingent on residence time of the species in the region, which was indicated by the significant relationship between species' altitudinal maxima and their residence times ($y = 2.17x + 491.3$; $F = 18.9$; df = 1, 63; $P < 0.0001$; on average, species spread by 16.1 ± 45.3 altitudinal m/y between 1738 and 1986). The same relationship for altitudinal minima was nonsignificant ($F = 1.0$; df = 1, 63; NS). This is because factors that constrain invasions to higher altitudes (i.e., the abiotic stressful conditions in the mountains) (5, 13) are not relevant in low-altitudinal regions. This pattern of spread is likely to be valid and robust, despite the fact that the current distribution is definitely the result of multiple introductions into the country of the alien species analyzed. However, within the wider region of Central Europe, the species started to spread at approximately the same time (12).

These results show that higher altitudes were increasingly invaded by alien species introduced into the Czech Republic in the last 250 y. However, that species occur at higher altitudes and their altitudinal ranges are larger than in the past does not answer the question about whether this pattern is simply a consequence of the fact that neophytes introduced earlier had more time to spread into new areas than those that arrived later. Holding the effect of the other variable constant in multiple regression, both the year of the record and the year of species' introduction had a highly significant effect

Author contributions: P.P., V.J., J.P., and J.W. wrote the paper.

The authors declare no conflict of interest.

See companion article on page 656.

[1]To whom correspondence should be addressed. E-mail: pysek@ibot.cas.cz.

on the altitude of the individual records ($F = 112.5$; df = 2, 28,285; $P < 0.0001$), but the effect of the year of record was nearly seven times stronger (0.40 ± 0.03; $t = 13.37$; df = 28,285; $P < 0.0001$; slope ± SE) than that of the year of introduction (0.06 ± 0.02; $t = 3.36$, df = 28,285; $P < 0.001$). If the year of introduction were the main determinant of species' current altitudinal distributions (as is the case for current geographical distributions of alien plants in general) (12, 14), the process of colonization of higher altitudes could be largely attributed to a stochastic spread not affected by altitude.

However, the fact that there is a highly significant effect of the year of record when the effect of the year of introduction is held constant strongly suggests that spread to higher altitudes has become increasingly easier over the last two and a half centuries, a consequence of an interplay of several factors associated with altitudinal gradients in the temperate zone of Europe that were also changing over this period. These factors were the increasing disturbance associated with greater influence of humans at higher altitudes and increased propagule pressure (13, 15) as well as climate change manifested by an increase in temperature (16). Many invaders in Central Europe originate from warmer regions and thus are restricted by limited climatic suitability (17). Disentangling the roles of human-related and climatic factors along altitudinal gradient in driving colonization of alien plants at high altitudes is a promising topic for further studies.

ACKNOWLEDGMENTS. Funding was provided by Projects 206/09/0563 (Czech Science Foundation), AV0Z60050516 (Academy of Science of the Czech Republic), MSM0021620828 (Ministry of Environment of the Czech Republic), and LC06073 (Ministry of Environment of the Czech Republic). P.P. acknowledges support from a Praemium Academiae award from the Academy of Sciences of the Czech Republic.

1. Alexander JM, et al. (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proc Natl Acad Sci USA* 108:656–661.
2. Sobrino E, Sanz-Elorza M, Dana ED, González-Moreno A (2002) Invasibility of a coastal strip in NE Spain by alien plants. *J Veg Sci* 13:585–594.
3. Silva L, Smith CW (2004) A characterization of the non-indigenous flora of the Azores Archipelago. *Biol Invas* 6:193–204.
4. Arévalo JR, et al. (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspect Plant Ecol Evol Syst* 7:185–202.
5. Daehler CC (2005) Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities. *Perspect Plant Ecol Evol Syst* 7:203–216.
6. Moser D, et al. (2005) Environmental determinants of vascular plant species richness in the Austrian Alps. *J Biogeogr* 32:1117–1127.
7. Klinger R, Underwood EC, Moore PE (2006) The role of environmental gradients in non-native plant invasion into burnt areas of Yosemite National Park, California. *Divers Distrib* 12:139–156.
8. Palmer MW (2006) Scale dependence of native and alien species richness in North American floras. *Preslia* 78:427–436.
9. Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. *Preslia* 74:97–186.
10. Williamson M, Pyšek P, Jarošík V, Prach K (2005) On the rates and patterns of spread of alien plants in the Czech Republic, Britain and Ireland. *Ecoscience* 12:424–433.
11. Pyšek P, et al. (2004) Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53:131–143.
12. Pyšek P, Jarošík V (2005) Residence time determines the distribution of alien plants. *Invasive Plants: Ecological and Agricultural Aspects*, ed Inderjit (Birkhäuser, Basel), pp 77–96.
13. Dietz HJ, Edwards PJ (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology* 87:1359–1367.
14. Rejmánek M (2000) Invasive plants: Approaches and predictions. *Austral Ecol* 25:497–506.
15. Pauchard A, et al. (2009) Ain't no mountain high enough: Plant invasions reaching new elevations. *Front Ecol Environ* 7:479–486.
16. Millenium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: A Framework for Assessment* (Island Press, Washington, DC).
17. Pyšek P, Sádlo J, Mandák B, Jarošík V (2003) Czech alien flora and the historical pattern of its formation: What came first to Central Europe? *Oecologia* 135:122–130.