31 Airborne Migration of Obligate Nomads Demonstrates Gene Flow Across Eurasia

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31.1 Abstract

Understanding migration is important for the adequate use of biological resources. A new level of understanding is demonstrated with cereal pathogens recognized to be obligate nomads of the atmosphere. From basic reasoning, a hypothesis is put forward: virulence complexity, i.e. the number of virulences per pathogen genotype, is expected to increase in the direction of predominant winds. The hypothesis was confirmed by all of a variety of data from own investigations and from the literature and by modelling. For instance, virulence complexity of cereal mildews and rusts increased from western to eastern Europe and as far as Siberia by approximately one to two virulences per 1,000 km. The impact of our findings for general population genetics and gene flow across Europe and Asia and for further geographical areas is supposed to be considerable and worth elucidating further. *Obligate nomad* is a novel term that appears to be advantageous in several respects of population biology and life. Therefore, the consideration of obligate nomadism is extended to a spectrum of cases including plants, fungi and animals, as well as to neonomads and invasive plant species as a consequence of our present traffic and civilization. Most often obligate nomads are forced to migrate as substrates are ephemeral and ecological niches exist for a short period of time only. Chances and risks for health and the use of biological resources are discussed.

31.2 Migration and Obligate Nomads

Migration and biological resources have always been of major importance for human society. Repeatedly, migrating pests and pathogens on plants gave rise to

heavy losses and even catastrophes such as the great famine caused by potato blight and its fungus *Phytophthora infestans* (Day 1977; Dixon 1998). Migrating insects can either cause damage by themselves or serve as vectors of other organisms. Examples include Phylloxera caused by the aphid *Viteus vitifolii* attacking vineyards, and the potato beetle *Leptinotarsa decemlineata*, both reaching Europe from North America in the 19th century. More recently, Dutch elm disease caused by a fungus-beetle association has led to devastating elm decline in many European countries, and the pinewood nematode, again associated with a beetle, was disastrous in Japan. A well-known disease of wild and domestic rabbits caused by a virus is myxomatose, whereby, after introduction of a killer strain to Europe, mutants that were less severe pointed out to be of selective advantage and spread. Moreover, a number of invasive plant species as well as fungi have conquered many regions and even whole continents as neophytes since the Middle Ages, and many of the species pose threats to native flora and fauna. Their migration is well documented. For instance, spores of the fungus *Anthurus müllerianus* were introduced with military blankets from Australia during World War I; starting from the Netherlands this fungus spread throughout western Europe as far as Russia.

Quite a number of species are even forced to migrate and change their habitat in order to survive. Their reasons for moving are well known and quite different. Seasonal climate is one of them, often leading to the temporary loss of living conditions. Moreover, a number of heterotrophic organisms are adapted to unique and exceptional substrates exclusively used by them. Often, the substrates are ephemeral and only available for a short period of time. Therefore, these organisms have transitory habitats only and need to find new substrates frequently. In a recent study of plant pathogens, those species that need migration to survive were called *obligate nomads* (Limpert et al. 1999).

A closer look at these pathogens and their cereal hosts appears to be adequate, as well as an analysis of the forces of, e.g. *dispersal* and *virulence* which are important for host-pathogen systems, because such systems may provide a model for so many systems of interacting organisms in general. Finally, we will widen the scope towards a general look at obligate nomads, including neonomads.

Cereals including their wild relatives are major biological resources around the world. The rusts and mildews living on them are important wind-dispersed pathogens (Oerke et al. 1994; Limpert and Bartoš 1997; Hau and de Vallavieille-Pope 1998). The barley mildew pathogen caused by *Blumeria (Erysiphe) graminis* f.sp. *hordei*, as well as the leaf rust pathogen on wheat, *Puccinia triticina*, have been extensively studied (Bartoš et al. 1996; Park and Felsenstein 1998; Limpert et al. 1999; Mesterházy et al. 2000). In the present context it is worth stressing that they are obligate parasites which need living hosts to survive.

Living on ephemeral tissue only, these cereal pathogens frequently change their habitat. Starting from a number of points of interest concerning dispersal (Andrivon and Limpert 1992; Hau and de Vallavieille-Pope 1998; Aylor and Irvin 1999; Brown and Hovmöller 2002), it is our aim here to focus further on the understanding of population biology and wind dispersal in particular, and its possible relevance for strategies to use the cereal hosts in time and space (Limpert et al. 1999, 2000; Limpert, unpubl. data).

So far, the term wind dispersal is generally used without further specification. However, wind dispersal is worth differentiating as it can affect populations of organisms quite differently. A key to the understanding is, as briefly mentioned above, the longevity of the organisms, depending on their conditions of life. Despite wind dispersal of spores, life of e.g. the basidiomycete *Armillaria* can remain quite sedentary due to perennial mycelium in soil and decaying wood. Ergot on rye, in contrast, is an obligate nomad once a year, when spores have to reach the seed vessel of a rye ear. Wheat leaf rust and barley mildew in northwestern Europe are obligate nomads as well and, moreover, highly mobile as they change their place of living almost 10 and even more than 20 times per year, respectively, (Limpert and Bartoš 1997).

Changing the place of living also means pathogen attack which often creates considerable losses in crop quality and quantity. Losses can be avoided through the use of chemicals or, ecologically safer, through the use of genes conferring resistance in the host. As a genetic consequence, there will be selection of chemical resistance or pathogen virulence that re-allows the pathogen to grow. Thus, as a general consequence, dispersal means selection (Flor 1946; De Wit 1992; Limpert et al. 1996, 1999, 2002). As another established consequence, virulence complexity (as well as fungicide resistance complexity), i.e. the number of virulences per pathogen genotype, increases with time (Munk et al. 1991). Therefore, virulence complexity is worth considering in strategies to improve the use of host resistance and to reduce the selection of super-races able to attack most or all cultivars. Much less established are the consequences for the evolution of virulence complexity in space, with migration favored in one direction.

Cereal pathogens are well suited for a corresponding investigation. Evidently, for migrating humans, language knowledge can be beneficial and of selective advantage. Similarly, from knowledge of meteorology, aerobiology and population genetics, the hypothesis was derived that virulence of nomadic pathogens increases with predominant winds (Limpert et al. 2002). In corresponding studies, virulence complexity was analysed for different pathogens using established procedures of pathotype (or race) analysis. Spores of the barley mildew pathogen were sampled and analysed according to Limpert et al. (1984, 1990), Müller (1993) and Müller et al. (1996). Representative samples were obtained on the motorway by driving across regions of interest for cereal production in Europe, with a jet spore sampler mounted on the car roof. Petri dishes with fresh leaf segments were exchanged after approximately 100 km, taking into account the use of barley varieties and regional agroecological conditions. The sample size was close to 2000 isolates per year in regions north of Geneva. The virulence spectrum of individual genotypes that developed after incubation was analysed on leaf segments on agar under controlled conditions on differential sets consisting of near-isogenic lines (NILs) (Kolster et al. 1986). For leaf rust, data from the literature were re-evaluated. Methods were based on either those for barley mildew, with 20 NILs plus 5 differential cultivars (Park and Felsenstein 1998), or field sampling and 15 NILs (Mesterházy et al. (2000)).

Host-pathogen systems on cereals are unique: nowhere else appears to be more biomass produced that is genetically more uniform. Thus, the reverse of the well-

known problems of genetic uniformity and vulnerability of the crop is that the corresponding systems can be excellent models to analyse population patterns and gene flow and their effects on biological resources, in order to develop adequate strategies to solve the problems.

Thus, in addition to (1) specifying the effects of wind dispersal, we (2) modelled the dispersal effects on the evolution of virulence complexity in space, (3) analysed comprehensive pathogen samples in time and space throughout Europe, and (4) re-evaluated data from the literature; moreover, we (5) extended the scope to further obligate nomads with reference to fungi, lichens, mosses and plants, and discuss our findings concerning chances and risks for plant, animal and human health and for the use of biological resources.

31.3 Eurasian and Further Paths of Population Genetics

What are the consequences of obligate nomadism in corresponding models and reality? The air over Europe up to 600 m above ground moves on average some 10 km/h eastward, a movement that is thought to continue throughout Asia (Limpert et al. 2000; Graber and Limpert, unpubl.). Therefore, we modelled the effects of predominant winds and obligate nomadism for a selected trait over three successive regions. With one selection cycle of the pathogen per region, virulence complexity increased consistently and considerably by 0.25 virulences per step and selection cycle, from 1.5 virulences originally to 2.25 in the end (Fig. 1).

There are a number of data sets consistently demonstrating the increase of virulence complexity in the direction of major dispersal. Early observations of the barley mildew pathogen across Europe go back to the beginning of the 1980s (Limpert et al. 1999; Limpert, unpubl.). During an initial phase, western and central Europe were thought to be one unit of population genetics in this respect (Limpert et al. 1996). However, we soon learned that it is worth separating Great Britain from continental Europe. Both areas independently exhibit the phenomenon described.

Much to our surprise, the phenomenon was even better expressed both in degree and consistency (R^2) on the island of Great Britain, which can be due to the canalizing effect of the island shape, with predominant dispersal from Scotland to England. This demonstrates the presence of a *Scottish-English path of population genetics*. In comparison, the path considered on the continent is much wider, with conditions for host and pathogen being more diverse (Limpert et al. 2000, and unpubl.). A far-reaching question and hypothesis was put forward for continental Europe and Asia recently: "Does virulence accumulate along the way from Paris to Beijing?" (Limpert et al. 2000, 2002). Impressive data sets for leaf rust are available for this area in the literature (Chester 1946; Park and Felsenstein 1998; Mesterházy et al. 2000).

Historical data (Chester 1946) are, after re-evaluation (Limpert et al. 2000, 2002), in agreement with the hypothesis of a *Eurasian path of population genetics* that is supported by recent data. Virulence complexity of rust isolates in Europe

was studied in 1998 with data from five countries (Mesterházy et al. 2000). Based on predominant pathotypes, virulence complexity again increased from France (close to 2) to Poland (approximately 7; Limpert et al. 2002). In addition to the west-east gradient, a north-south gradient of increasing virulence complexity becomes obvious here. This can be due to climatic conditions favoring epidemics and, as a consequence, an increased number of host resistance genes used in the south. Similar and other effects cannot be excluded in the west-east direction either, in some contrast to conditions for mildew attack that are best in the maritime climate of the northwest. Further results from Europe of interest for the concept come from crown rust of oats caused by *Puccinia coronata* and are currently being re-evaluated (Šebesta et al. 1999; Šebesta, unpubl.).

Fig. 1. Effects of wind dispersal and selection on virulence complexity, *vc*, of a nomadic pathogen: a model. Indicated is, from *left to right*, the initial composition of the pathogen population consisting of eight pathotypes with a frequency of 12.5% each, and changes after selection in three successive regions; 50% of the host is sensitive, the remainder resistant, with *R*-gene 1, 2, and 3 (*R*-1, *R*-2, *R*-3) present in regions 1, 2, and 3, respectively

Most impressive are comprehensive data on leaf rust of wheat from the area north of Geneva, where virulence complexity increases quite steadily from less than 4 in western France to approximately 7 in Poland, and more than 14 in Siberia close to Omsk (Park and Felsenstein 1998, re-evaluated by Limpert et al. 2002). Although most data are from the beginning of the Eurasian wind path, the effects on population genetics and gene flow for the entire area appear evident. Of course, there is a considerable way left from Omsk to Beijing. However, due to major conditions remaining the same, i.e. predominating winds from the west and presence of the host, the conclusion of virulence complexity increasing along the way from Paris to Beijing appears to be justified and important enough to merit

further consideration. The Scottish-English path of gene flow and population presumably appears to be but one additional case worth knowing and considering.

How do spores migrate? As spores start from plants, concentrations of viable units are highest close to ground level. Many short distances covered per life cycle of these polycyclic diseases are thought to sum up to long-distance migration in the end (Limpert et al. 1999). Presumably the conditions are similar to those of gene flow via pollen concluded from population genetic studies of Pinaceae (Ziegenhagen et al., this Vol.). Single-step, long-distance transport of viable spores may occur occasionally in or below clouds protecting against UV radiation, as is the case with dust clouds and interhemispheric transport of viable microorganisms (Prospero, this Vol.).

31.4 Obligate Nomads: Extending the Scope

The phylogenetic old kingdoms of organisms, fungi and mosses were very early land-inhabiting organisms living as obligate nomads. The reasons for moving are quite different for today's vegetation. One is that the substrates of the heterotrophic organisms are rare and used up so quickly that new ones have to be found frequently. Plants and fungi have to reach new places with spores or seed. In areas with seasonal climate, the growing conditions can restrict the organisms to a short life cycle only. However, also in tropical rain forests with continuous climate, host-dependent organisms have great difficulty in finding the next host. This is due to the high degree of diversity causing large spaces between individuals of the same species and substrates in these habitats (Kost 2004).

Some of these very ephemeral substrates are only available for a short period. As with the cereal rusts and mildews, epiphytes and even more so epiphylls lose their habitat if the life cycle of the plant or the leaf is terminated. More than half the tropical plants depend on such habitats. Liverworts, lichens, fungi and algae living as epiphylls are adapted to this nomadic way of life in tropical rain forests.

Dung of various chemistry and ecology spread by animals is another prominent example of ephemeral substrate. Dung is very interesting for a number of so-called coprophilous organisms due to its high content of nutrients and especially nitrogen (Ellis and Ellis 1988). Dung beetles and many other species from different kingdoms are well known. The main problem of important fungi and mosses, however, is how to reach the new substrates. This is achieved through an intricate dispersal biology in harmony with the erratic substrate occurrence (Yu and Wilson 2001). One trick to cope with the problem is to enter the digestion system of the dung producer. To this end, the spores of the dung fungus have to get from the place of production to the area of browsing or grass consumption by the animal. This can be done by active discharge and wind-dispersed spores of the fruiting bodies of these asco- and basidiomycetes. Indeed, the ejection of the spore balls of *Pilobolus* is so effective that even some nematodes use it as a means to reach the new host (Eysker 1991).

A more efficient method of transport from one “oasis” to the next is to use “camels”, like human nomads do. In the case of fungi and mosses, the transfer will be made by insects attracted by conspicuous fruiting bodies. Gluing spores adhere to the chitin surface or water droplets filled with spores are sucked in by flies. Dung mosses like genera of the Splachnaceae have spore capsules with enlarged apophysis which can be remarkably colored. This attraction can serve as a landing place for insects. Thus, interestingly enough many of the coprophilous mosses are entomophilous, enhancing the probability of spore dispersal in appropriate dung habitats by coprophilous insects (Marino 1991).

Cystofilobasidium capitatum is an extremely specialized coprophilous fungus (Oberwinkler et al. 1983). This very rare mycoparasite only lives inside apothecia of dung-inhabiting Ascomycota. Thus, the nomadic way of life of this species is threatened also, as it combines the low availability of the coprobic substrate with the short life span of an ascoma of a dung fungus.

Fruiting bodies of fungi are, again, isolated substrates for many organisms. Insects, imagines or larvae of flies and beetles develop inside them. Specialized mycoparasites use the carpophores as nutrient sources (Helfer 1991) and a high diversity of species is closely adapted to such systems. Mycoparasitism of the ephemeral fruiting bodies is described from many asco- and basidiomycetes. *Spinellus fusiger* (zygomycetes) produces sporangiophores on the surface of the tiny cap of *Mycena* sp. *Tremella* species select as species-specific substrate lichens, *ascomycetes*, *dacrymycetales*, *Stereum* species or other wood-inhabiting *aphyllophorales*.

The fungal fruiting bodies can be infected by nomadic species of all classes of fungi such as:

- Basidiomycota (*Asterophora*, *Atractiella*, *Chritiansenia*, *Collybia p. pte.*, *Cryptomycocolax*, *Cystofilobasidium*, *Nyctalis*, *Platyglaea*, *Tremella*, *Volvariella p. pte.*)
- Ascomycota (*Hypocreales*, *Cordyceps p.pt.*, *Orbiliaceae p. pt.*, *Mycogone rosea*)
- Zygomycota (*Spinellus*, *Syzygites*)
- Deuteromycota (many species).
- Myxomycota (*Bahamia spp.*)

Fungal parasites of insects survive similarly. After digestion of the larvae or imago the substrates are depleted. In most cases, the fungal life turns into a spore production phase with an additional spore discharge. This behaviour is widespread and most organisms act in this way, if the substrate is used. Only through nomadism can a new basis of nutrition be found. It is very obvious that the sexual stage is produced exactly at that phase of life, before the beginning of the nomadic phase, thus creating additional diversity of advantage for survival in an unknown future.

Many fungal species depend on specific and rare substrates to be digested by them (Alexopoulos et al. 1996, Kirk et al. 2001). So they are forced to find new bases for surviving. This can be observed many times, for example in the wood

decomposer which only inhabits selected parts of specific tree species, which have a definite age and which grow under definite climatic conditions.

An unusual growing place of mosses and fungi is charcoal and old fireplaces (Ellis and Ellis 1988). In natural habitats these carbonicolous organisms regularly appear after forest fires. As one of the first plants, *Funaria hydrometrica* regularly covers this heat-sterilized and dead habitat with small gametophytes. At the same time some carbonicolous fungi (*Anthracobia* spp., *Geopyxis carbonaria*, *Rhizina undulata*, *Plicaria* spp., *Myxomphalina maura*) appear in these places. To spread they utilize the sterile areas with reduced competition from other organisms. These species are able to live there, however, only during the short initial phase of these disturbed areas. As soon as other plants and organisms start recolonizing these places the carbonicolous mosses and fungi disappear.

Of course, deserts are extreme habitats and life needs to be highly adapted. During the dry periods fungi and mosses usually cannot grow. One survival strategy of mosses is to dry up and stop life activities until enough humidity refreshes them. Another strategy of mosses and fungi is to complete the life cycle during the few weeks that the desert is wet enough (Düring 1979). Conversely, both groups of organisms produce drought-resistant spores with thick walls. They will be dispersed by sandstorms over hundreds of kilometers and germinate as soon as conditions for life are better again. Desert Basidiomycota with ephemeral fruiting bodies are members of the genera *Agaricus*, *Agrocybe*, *Coprinus*, *Psathyrella*, *Psilocybe* and *Stropharia* (Kost, unpubl. data).

A well-known group of nomadic plants in steppe vegetation is adapted for distribution as whole plants by wind (*Eryngium*, *Falcaria vulgaris*, *Seseli* div. spec., *Phlomis pungens*, *Centaurea diffusa*, *Salsola kali*, *Gypsophila paniculata*; Walter and Breckle 2002). Due to their distribution dynamics some of these plants also form well-defined geoelements (Turano-Saharan elements). Striking cases of nomadic plants are also adapted to unusual ecological events like fire, land slides, etc. The case of *Funaria hygrometrica* is well known: the basis for the nomadic occurrence is fire, also on rather small spots caused by human activity. Further members of this well-defined community, all based on high demand for nitrogen, are *Ceratodon purpureus*, *Marchantia polymorpha* and *Lunularia cruciata*.

The semi-saprophyte *Buxbaumia aphylla* occurs nomadically and extremely sporadically in disturbed forest habitats, usually caused by big fires (Jones 1970; Wiklund 2002, 2003). *Geranium bohemicum* is an extremely rare nomadic species in forests, occurring only after big fires (Granstrom 1993). One explanation for its surprising presence is its extraordinary capability to produce seeds that can survive in soils for more than 100 years (Milberg 1994).

A number of neonomads can be regarded as obligate nomads of today's traffic and civilization. Such invasive plant species have conquered many regions and indeed whole continents, and many of the species pose threats to native flora and fauna. Agronomists and ecologists use the terms *weed* and *weediness* in different ways, and this is often a source of misunderstanding, especially in discussions concerning the release of transgenic plants. For agronomists, the problem of weediness is solved if the aggressive weed can be removed from the agrosystem

by means of adapted measures. They are not interested in its behavior outside of agrosystems, i.e. in (semi-)natural habitats.

From the ecologist's perspective, invasions of weeds into (semi-)natural plant communities are potentially risky. Highly competitive invaders are able to disturb the pattern of species. As a result, rare indigenous species of tropical islands, of regions and even continents with an old flora, only weakly influenced by migrations of the last few millennia, are often weak competitors, and can be eliminated or markedly reduced in coverage. In worst case scenarios, the invader succeeds in occupying the entire surface of certain areas as a near monoculture, this at least for several years or decades until new and 'natural' enemies fight back. Maybe seemingly less dramatic, but for the eyes of trained field ecologists still worrying, are dynamic situations where ecological niches are invaded, precisely wiping out rare indigenous species. This can happen (and unfortunately has happened in the past) with ecological dynamics which is triggered off by agriculture and horticulture (Ammann 1997, 2000). A typical example of an agricultural weed is the globally distributed *Galeopsis tetrahit*, an allotetraploid, derived from two rather tame species, *G. pubescens* and *G. speciosa* (Müntzing 1930).

A balanced discussion on the fate of exotic (and thus potentially invasive) species in agricultural habitats is given by Meiners et al. (2002). Agricultural practices may also influence the future impacts of exotics. Frequent plowing associated with row-crop agriculture prevents the accumulation of exotic perennial cover. When these sites are abandoned, both natives and exotics start invading at the same time, resulting in a plant community that does not show significant effects of exotic species. In contrast, agricultural practices with repeated biomass removals such as hay fields, meadows and grazing result in perennial exotic communities that resist invasion by other species (Mack and D'Antonio 1998). These effects may persist for 15 years or more. One-time plowing was not sufficient to reduce the impacts of these species on community development at these sites. It is important to note that it is not the invasion of an exotic plant, per se, that reduces species richness but the dominance of a patch by exotic species which may result in reduced species richness. Species richness of natives and exotics is positively associated, showing no effects of exotic invasion on native species richness. However, when exotic plants make up a large proportion of the total cover of a plot, we observed reductions in community richness (Meiners et al. 2001). Therefore, managers should focus control efforts on species that have the potential to dominate local plant communities.

Some lichen species as well as many moss species are extreme niche specialists and can be regarded as nomadic in their dispersal and reproduction biology. Lichens, for instance, can reproduce very effectively by soredia units. Soredia are vegetative reproductive structures that contain hyphae and algal cells. They break off the parent thallus, are dispersed by various agents, and produce new lichens in a new specific niche location. They are tiny structures that form in the medulla and break through the upper cortex to erupt on its surface, which can be easily blown by wind or washed off by water. Another lichen, *Lecanora esculenta*, known in the Bible as Manna, is basically a crustose and saxicolous species,

which can break off in dry conditions and eventually assemble in desert depressions as edible Manna used to feed animals (Donkin 1981).

31.5 Conclusions and Outlook

A number of species belong to the group of obligate nomads. For the host-pathogen systems focused on in this chapter, a hypothesis was put forward according to which virulence, the character under selection, and virulence complexity in the pathogen population should increase in the direction of predominant dispersal (Limpert et al. 2002). A prerequisite is diversity for the trait considered in both the host (where single genes are sufficient) and the pathogen (which needs complex genes). Being endemic over vast geographic areas covering several continents contributes to the diversity present even at the local scale. The hypothesis based on fundamental logic is well supported by modelling and comprehensive results both from our own investigations and from the literature after re-evaluation.

Dispersal is selection. As a consequence of predominant dispersal in one direction there appears to be a *Eurasian path of population genetics and gene flow* along which genes and genotypes move, as well as, presumably amongst others, a *Scottish-English path*. Along these paths, pathogen composition and evolution should be predictable to a certain degree. There are important conclusions for disease resistance: where to find the most valuable resistance sources (downwind) and how to make the best use of host resistance (shifting the culture of hosts with a certain resistance gene upwind). Moreover, the hypothesis throws new light on the question of costs of unnecessary virulence. These and further conclusions have been described elsewhere in more detail (Limpert and Bartoš 2002).

Obviously, in addition to wind, further factors such as virulence combinations, climate and temperature or alternate hosts can affect virulence complexity in various ways and would thus benefit from further analyses. Warmer climate, for instance, is more favorable for wheat leaf rust in eastern Europe, whereas the opposite is true for cereal mildews. Moreover, the co-evolutionary processes with epidemic dynamics in natural populations would also be worth studying for the effect on virulence complexity, both from the regional to the pandemic scale.

One very general finding appears worth stressing: presumably, there is no other biomass produced around the globe as big and genetically uniform as that of cereals. As a consequence, this should be true also for the biomass of their pathogens. Host pathogen systems involving cereals are thus supposed to have a pilot function for the recognition of interacting systems in general.

Evidently, dispersal affects populations of species in different ways, depending on the degree of nomadism. What about the other obligate nomads, neonomads, invasive plant species and interacting systems mentioned, such as, e.g., the highly complex coprophilous systems of mosses, fungi and insects? Do they have genes of selective advantage for migration too, and genes affecting gene flow? Can the same or similar rules of interaction be recognized? Presumably, for most of the questions we merely do not yet know the answer.

What are typical traits of the extremes, highly mobile obligate nomads on the one hand, and highly sedentary counterparts on the other? What are typical traits of successful neonomads, and what would be the consequences of knowing them, amongst others, for the use of biological resources, and for measures of quarantine and practice?

Of course, the hypothesis should be of importance not only for plant health, but also for human and animal health, and for further populations affected by wind such as species of insects, amongst others those causing malaria (Limpert and Bartoš 2002). Also spiders are known to travel by wind, and even some crustaceae living in temporary waters like certain *Ostracodae*: their eggs appear to be as easily wind-dispersed as are mildew spores (Vieberg pers. com.).

Fascinating challenges are ahead of us, leading to novel insight into geobiology and geo-medicine. Evidently, there is the need to quantify nomadism. Perhaps the most striking questions of today, however, relate to viruses (Shortridge and Stuart-Harris 1982; Drosten et al. 2003, Guan et al. 2003; WHO 2004; Becker, this Vol.). Does the Eurasian path of population genetics and gene flow exist for them too?

Foot and mouth disease is known to spread through the air (Donaldsen et al. 2001). How is the viability of coronavirus spreading SARS by air and of the causal agent of human and avian influenza, with a number of further hosts? Even if outdoor conditions were unfavorable in general, it might have been sufficient for the evolution of influenza over the last thousands of years if conditions were favorable for aerial spread once per month, or per year, or even per 5 or 10 years.

China and East Asia are thought to be the origin of influenza pandemics around the world (Shortridge and Stuart-Harris 1982), and they were the origin of both SARS (Drosten et al. 2003, Guan et al. 2003) and the present avian influenza A(H5N1) (WHO 2004). This is in line with our concept predicting that the most dangerous pathogens gather and evolve at the end of this *Eurasian path of population genetics*.

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31.6 References

- Alexopoulos CJ, Mims CW, Blackwell M (1996) Introductory mycology. Wiley, New York, 868 pp
- Ammann K (1997) Botanists to blame? Plant Talk, 4
- Ammann K, Jacot Y, Rufener Al Mazyad P (2000) Weediness in the light of new transgenic crops and their potential hybrids. J Pl Dis Prot, Special Issue 19-29
<http://www.botanischergarten.ch/debate/weeds1.pdf>
- Andrison D, Limpert E (1992) Origin and proportions of components of populations of *Erysiphe graminis* f.sp. *hordei*. J Phytopath 135:6-19
- Aylor DE, Irvin ME (eds) (1999) Aerial dispersal of pests and pathogens. Spec Issue. Agric For Meteorol 97:233-252

- Bartoš P, Stuchlíková E, Hanušová R (1996) Adaptation of wheat rusts to the wheat cultivars in former Czechoslovakia. *Euphytica* 92:95-103
- Brown JKM, Hovmöller MS (2002) Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* 297:537-541
- Chester KS (1946) The nature and prevention of the cereal rusts as exemplified in the leaf rust of wheat. *Chronica Botanica*, Waltham, Massachusetts
- Day PR (ed) (1977) The genetic basis of epidemics in agriculture. New York Academy of Sciences, New York, 400 pp
- De Wit PJGM (1992) Molecular characterization of gene-for-gene systems in plant-fungus interactions and the application of avirulence genes in control of plant pathogens. *Ann Rev Phytopathol* 30:391-418
- Dixon B (1998) The fungus that made John F Kennedy president, and other stories from the world of micro-organisms (in German). Spektrum Akad, Berlin
- Donaldson AI, Alexandersen S, Sørensen JH, Mikkelsen T (2001) Relative risks of the uncontrollable (airborne) spread of FMD by different species. *Vet Rec* 148:602-604
- Donkin RA (1981) The Manna lichen - *Lecanora-Esculenta*. *Anthropos* 76:562-576
- Drosten C, Gunther S, Preiser W, van der Werf S, Brodt HR, Becker S, Rabenau H, Panning M, Kolesnikova L, Fouchier RA, Berger A, Burguiere AM, Cinatl J, Eickmann M, Escrion N, Grywna K, Kramme S, Manuguerra JC, Muller S, Rickerts V, Stürmer M, Vieth S, Klenk HD, Osterhaus AD, Schmitz H, Doerr HW (2003) Identification of a novel coronavirus in patients with severe acute respiratory syndrome. *N Engl J Med* 348:1967-1976
- Düring HJ (1979) Life strategies of Bryophytes: a preliminary review. *Lindbergia* 5:2-18
- Ellis MB, Ellis PJ (1988) Microfungi on miscellaneous substrates. Croom Helm, London, 244 pp
- Eysker M (1991) Direct measurement of dispersal of *Dictyocaulus viviparus* in sporangia of *Pilobolus* species. *Res Vet Sci* 50:29-32
- Flor HH (1946) Genetics of pathogenicity in *Melampsora lini*. *J Agric Sci* 73:335-337
- Granstrom A (1993) Spatial and temporal variation in lightning ignitions in Sweden. *J Veg Sci* 4:737-744
- Guan Y, Zheng BJ, He YQ, Liu XL, Zhuang ZX, Cheung CL, Luo SW, Li PH, Zhang LJ, Guan YJ, Butt KM, Wong KL, Chan KW, Lim W, Shortridge KF, Yuen KY, Peiris JSM, Poon LLM (2003) Isolation and characterization of viruses related to the SARS coronavirus from animals in Southern China. *Science* 10:1126/Science 10:87139
- Hau B, de Vallavieille-Pope C (1998) Wind-dispersed diseases. In: Jones DG (ed) *The epidemiology of plant diseases*. Kluwer, Dordrecht, pp 323-347
- Helfer W (1991) Pilze auf Fruchtkörpern - Untersuchungen zur Ökologie, Systematik, und Chemie. *Libri Bot* 1:1-157
- Jones EW (1970) Ecology of *Buxbaumia aphylla* Hedw. *Trans Br Bryol Soc* 6:139
- Kirk PM, Cannon PF, David JC, Stalpers JA (2001) *Ainsworth and Biby's dictionary of the fungi*. CAB International, Wallingford, 655 pp
- Kølster P, Munk L, Stølen O, Løhde J (1986) Near-isogenic barley lines with genes for resistance to powdery mildew, *Crop Sci* 26:903-907.
- Kost G (2004) Ecology and morphology of some tropical fungi (Contributions to tropical fungi II). In: Agerer, Blanz, Piepenbrinck (eds) *Frontiers in Basidiomycote Mycology*. IHW, Eching; in press
- Limpert E, Bartoš P (1997) Analysis of pathogen virulence as decision support for breeding and cultivar choice. In: Hartleb H, Heitefuss H, Hoppe H-H (eds) *Resistance of crop plants against fungi*. Fischer, Jena, pp 401-424
- Limpert E, Bartoš P (2002) Wind-dispersed nomadic pathogens - conclusions for disease resistance. *J Genet Plant Breed* 38:150-152

- Limpert E, Schwarzbach E, Fischbeck G (1984) Influence of weather and climate on epidemics of barley mildew, *Erysiphe graminis* f.sp. *hordei*. In: Lieth H, Fantechi R, Schnitzler H (eds.) Interaction between climate and biosphere. Progr Biomet 3, Swets & Zeitlinger B.V. Lisse, 146-157.
- Limpert E, Andrivon D, Fischbeck G (1990) Virulence patterns in populations of *Erysiphe graminis* f.sp. *hordei* in Europe in 1986. Pl Pathol 39:402-415.
- Limpert E, Finckh MR, Wolfe MS (eds) (1996) Integrated control of cereal mildews and rusts: towards co-ordination of research across Europe. Proc Worksh COST 817, European Commission, Luxembourg, 276 pp
- Limpert E, Godet F, Müller K (1999) Dispersal of cereal mildews across Europe. Agric For Met 97:293-308
- Limpert E, Bartoš P, Graber WK, Müller K, Fuchs JG (2000) Increase of virulence complexity of nomadic airborne pathogens from west to east across Europe. Acta Phytopath Entomol Hung 35:261-272
- Limpert E, Bartoš P, Buchenauer H, Graber WK, Müller K, Šebesta J, Fuchs JG (2002): Airborne nomadic pathogens: do virulence genes accumulate along the way from Paris to Beijing? Plant Prot Sci 38:60-64
- Mack MC, D'Antonio C.M. (1998) Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13:195-198
- Marino PC (1991) Dispersal and coexistence of mosses (Splachnaceae) in patchy habitats. J Ecol 79:1047-1060
- Meiners SJ, Pickett STA, Cadenasso ML (2001) Effects of plant invasions on the species richness of abandoned agricultural land. Ecography 24:633-644. <http://www.botanischergarten.ch/Weeds/Meiners-Ecography-2001-Effects.pdf>
- Meiners SJ, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography 25:215-223. <http://www.botanischergarten.ch/Weeds/Invasive-40years-Exp-Ecography.pdf>
- Mesterházy Á, Andersen O, Bartoš P, Casulli F, Csősz M, Goyeau H, Ittu M, Jones E, Manisterski J, Manninger K, Pasquini M, Rubiales D, Schachermayr G, Strzembicka A, Szunics L, Todorova M, Unger O, Vanco B, Vida G, Walther U (2000) European virulence survey for leaf rust in wheat. Agronomie 20:793-804
- Milberg P (1994) Germination of up to 129-year-old, dry-stored seeds of *Geranium-bohemicum* (Geraniaceae). Nord J Bot 14:27-29
- Munk L, Jensen HP, Jørgensen JH (1991) Virulence and disease severity of barley powdery mildew in Denmark. In: Jørgensen JH (ed) Integrated control of cereal mildews: virulence patterns and their change. In: Proc 2nd Eur Worksh on Integrated Control of Cereal Mildews, Risø National Laboratory, pp 55-65
- Müntzing A (1930) Outlines to a genetic monograph of the genus *Galeopsis*. Hereditas 13:185-341
- Oberwinkler F, Bandoni RJ, Blanz P, Kisimova-Horowitz L (1983) *Cystofilobasidium*: a new genus in the Filobasidiaceae. Syst Appl Microbiol 4:114-122
- Oerke EC, Dehne HW, Schönbeck F, Weber A (1994) Estimated losses in major food and cash crops. Elsevier, Amsterdam, 830 pp
- Park RF, Felsenstein FG (1998) Physiological specialization and pathotype distribution of *Puccinia recondita* in western Europe, 1995. Plant Pathol 47:157-164
- Šebesta J, Zwatz B, Roderick HW, Harder DE, Stojanović S, Corazza L (1999) Biological (genetic) control of fungal diseases of oat in Europe. Pflanzenschutz-Ber 58:152
- Shortridge KF, Stuart-Harris CH (1982) An influenza epicentre? Lancet 2:812-813
- Walter H, Breckle S (2002) Walter's vegetation of the earth: the ecological systems of the geo-biosphere, 4th edn. Springer, Berlin Heidelberg New York

- WHO (2004) Report on avian influenza A(H5N1).
http://www.who.int/csr/don/2004_02_13/en/
- Wiklund K (2002) Substratum preference, spore output and temporal variation in sporophyte production of the epixylic moss *Buxbaumia viridis*. *J Bryol* 24:87-195
- Wiklund K (2003) Phosphorus concentration and pH in decaying wood affect establishment of the red-listed moss *Buxbaumia viridis*. *Can J Bot* 81:41-549
- Yu DW, Wilson HB (2001) The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *Am Nat* 158:9-63