Taraschewski, H. 2006. Hosts and parasites as aliens. *Journal of Helminthology* 80: 99–128.
Torchin, M.E., K.D. Lafferty, A.P. Dobson, V.J. McKenzie, and A.M. Kuris. 2003. Introduced species and their missing parasites. *Nature* 421: 628–630.
Torchin, M.E., K.D. Lafferty, and A.M. Kuris. 2002. Parasites and marine invasions. *Parasitology* 124: S137–S151.

PARASITES, OF PLANTS

SEE PARASITIC PLANTS; PATHOGENS, PLANT

PARASITIC PLANTS

HENNING S. HEIDE-JØRGENSEN
University of Copenhagen, Denmark

Parasitic flowering plants exploit other flowering plants for water and nutrients with the help of one or more haustoria. Part of the haustorium, the intrusive organ, penetrates host tissue to establish contact with the conductive tissue of the host. Introduced parasitic plants occur throughout the world, and some are considered invasive. They often cause considerable economic damage when attacking monocultures in agriculture, orchards, and forestry, and much effort is spent to avoid and control invasive, harmful parasitic plants.

HISTORY

Parasitic flowering plants have been known and described since the days of Theophrastus. However, for a long time even esteemed botanists were doubtful about the nature of parasitic plants, and the class Sarcophytae was established for monstrous excrescences such as members of Rafflesiaceae and some Balanophoraceae; other plants were classified as fungi. In 1969 Job Kuijt published his *The Biology of Parasitic Flowering Plants*, for close to 40 years the only comprehensive book on parasitic plants. Intensive research on the physiology and control of harmful parasites began in the 1950s, when a witchweed, *Striga asiatica*, was introduced into the United States and threatened the cultivation of maize.

NUMBER AND TYPES OF PARASITIC PLANTS

With one possible exception among gymnosperms (*Parasitaxus usta* in New Caledonia), parasitic plants are limited to eudicotyledons with about 4,500 species in about 280 genera belonging to 20 families. The majority, about 4,100 species, are hemiparasites (i.e., they are green plants meeting most or all of their needs for carbon through their own photosynthesis). Hemiparasites may be attached to roots and called root parasites. In this case, water and other nutrients are achieved partly from the soil through the roots and partly from the host through haustoria. If hemiparasites are attached to stems (and consequently called stem parasites), then they obtain all water and inorganic nutrients from the host. A minority of about 390 species are holoparasites (i.e., they lack chlorophyll and photosynthesis); hence, carbon must be obtained along with water and other nutrients from the host. Holoparasites may also be either root parasites or stem parasites. A few holoparasitic root parasites develop a reduced root system that may contribute to water and nutrient absorption, but this is not well established.

Parasitic plants may be either facultative or obligate parasites. The latter cannot survive without a host, while the former may survive for a longer period and even produce some seeds, but productivity is better when water and organic and inorganic nutrients are supplied from one or more hosts. Only hemiparasitic root parasites can be facultative parasites. However, there are no records from nature of a parasitic flowering plant that has completed at least part of its life cycle without haustorial connections to host plants. Competition from other species in the plant community will sooner or later eliminate a potential facultative parasite. Therefore, the terms facultative and obligate should be avoided until facultative parasites have been demonstrated to occur in nature. They may be used under laboratory conditions where it is possible to grow some hemiparasitic Orobanchaceae throughout the reproductive phase without a host.

There are parasite “lookalikes.” These may be green orchids, bromelias, or ferns sitting on tree branches, but they neither develop haustoria nor obtain nutrients or water from the branches supporting them. Such plants are called epiphytes. Other “lookalikes” have lost all or nearly all chlorophyll and therefore look like holoparasites, but they have a three-part relationship wherein a mycorrhizal fungus interconnects the chlorophyll-free plant with a normal green plant having photosynthesis. Such plants used to be called saprophytes but are now called mycoheterotrophic plants (mycotrophic) plants. Examples are *Monotropa*, *Sarcodes*, some *Pyrola*, and orchids such as *Neottia nidus-avis* and *Corallorhiza trifida*.

HAUSTORIA

The development, structure, and function of the haustorium are essential subjects—as Job Kuijt has put it, “the haustorium is the *defining* part, the *essence* of parasitism.”

From Daniel Simberloff and Marcel Rejmánek, editors, *Encyclopedia of Biological Invasions*,
Berkeley and Los Angeles: University of California Press, 2011.

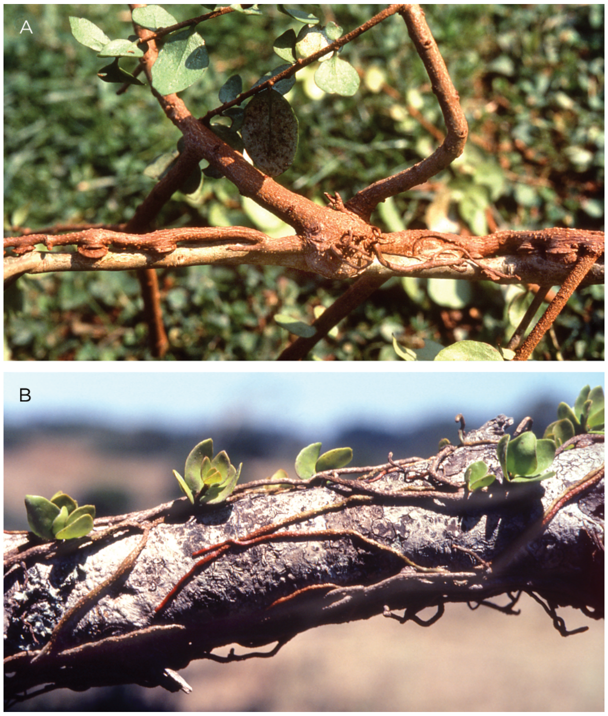

FIGURE 1 *Notanthera heterophylla* (Loranthaceae), Chile. (A) shows the adhesive disc of a primary haustorium (center) and several secondary haustoria on two cortical roots running parallel with the host branch. (B) shows several cortical roots with young leafy shoots emerging above secondary haustoria. (Photographs courtesy of Job Kuijt. Reproduced from H.S. Heide-Jørgensen, 2008.)

Available space does not allow for many details. From a developmental point of view, there are two types of haustoria, primary and secondary. The primary haustorium (Fig. 1) develops directly from the primary root apex; in the more advanced parasites, it is the only haustorium, and functions throughout the lifetime of the parasite. Evolution of the primary haustorium made holoparasitism possible, because the generally small-seeded holoparasites need water and nutrients from a host immediately after germination. Secondary haustoria (Fig. 1) develop on lateral and adventitious roots, and they may be short-lived, sometimes living only a few months. They may occur in numbers of up to several hundred per plant. Regarding nutrient absorption, it may be an advantage to have the secondary haustoria placed on roots from different hosts, because different hosts absorb various nutrient ions in varying amounts.

A haustorium may consist of an outer part called a holdfast with an adhesive surface used for preliminary attachment to the host. Within the holdfast, an intrusive organ develops, which penetrates the outer layers of the holdfast and then penetrates the host by a combination of enzymatic dissolution of cell walls and mechanical compression of cells. When the intrusive organ reaches the conductive tissue of the host, a bridge of xylem cells differentiates and connects host xylem with parental xylem of the parasite. The parasite always maintains a lower water potential than the host. The main route for water and nutrients from host to parasite is through the xylem bridge, although the complete interface between the two partners also plays an important role in nutrient uptake. In the most advanced holoparasites, the intrusive organ comprises all vegetative tissue of the parasite. It splits into cellular strands, which penetrate large parts of the host, although they rarely reach the shoot tips. This internal tissue is called the endophyte, as opposed to the exophyte for external parts such as shoots and flowers.

SYSTEMATIC AFFINITY OF INVASIVE PARASITES

Introduced invasive parasites are known from 5 or 6 of 20 families, including parasites. Most important are Orobanchaceae, a family that now also includes parasites earlier placed in Scrophulariaceae, and Convolvulaceae (*Cuscuta*); there are further examples in Loranthaceae, Viscaceae, and Santalaceae. The majority of invasive species are hemiparasitic, mostly annual root or stem parasites. Invasive holoparasites are known only from Orobanchaceae, and they are annual root parasites.

HOST RANGE

Parasitic flowering plants only occur as introduced species when acceptable hosts are available. Parasites with one or few acceptable hosts have no possibility of becoming introduced or invasive outside the natural distribution of their hosts unless the hosts also become introduced. To predict the possibility of a species becoming introduced, it is necessary to know the range of its acceptable and preferred hosts, a factor that is often underestimated. If a parasite is not found on a certain species, this species may still be an acceptable host. The reason for the absence may be ecological, such as the lack of a suitable dispersal agent (e.g., birds), or may have to do with other environmental conditions (e.g., the light conditions may be insufficient for the parasite). In bird dispersal, the proper bird species must be available. When present, their flying behavior is important (e.g., many birds prefer to search for food, rest, and seek nesting possibilities in hedges, solitary trees, or wood edges, while the inside of the forest may be avoided). For root parasites, it may be physically impossible to follow a host root with attached haustoria back to the mother plant. In herbarium collections, the host species is rarely identified and noted.

Host range varies from one acceptable host (e.g., the dwarf mistletoe *Arceuthobium minutissimum* on *Pinus griffithii*) to at least 343 different host species for the loranth *Dendrophthoe falcata*. In general, holoparasites have fewer hosts than hemiparasites. To be counted as a host, the species must be able to support the parasite throughout its life cycle. Genetics and biochemical tissue incompatibility determine the maximum number of acceptable hosts, but in practice parasite range is mainly influenced by geographical (host distribution) and ecological (dispersal biology and environmental factors) relationships.

BIOLOGY OF INVASIVE PARASITES

Generally, perennial parasites reduce the vigor of the host but do not kill the host, because to do so would destroy the possibility for survival of the parasite. A weakened host produces fewer flowers, fruits, and viable seeds and is more susceptible to fungal diseases and harmful insects. However, annual parasites can allow themselves to kill the host, provided seed set is completed before the host dies. Therefore, some of the most harmful invasive parasites are annuals. As mentioned, dispersal biology and host distribution limit the possibility of a parasite's becoming introduced and invasive. When a parasite becomes introduced, the dispersal agent has often been humans, whether deliberately (as for *Viscum album*, see below) or accidentally.

Loranthaceae

This family contains more than 900 species of hemiparasitic stem parasites and three root parasites, mainly from tropical and subtropical regions. Flowers are generally showy, and birds pollinate the flowers and disperse the fruits. Host range is generally high. Only a few species are considered introduced on some tropical islands in Southeast Asia (e.g., the aforementioned *Dendrophthoe falcata*). However, several loranths act like invasive species in orchards and plantations of monocultures. In India, *D. falcata* causes enormous damage in plantations of teak (*Tectona grandis*), and the parasite may lead to death of entire trees. One reason for the success of *D. falcata* on teak may be that it is more shade-tolerant than most other loranths. On average, the parasite receives only 40 percent of the light received by the host, and it will survive even when the host leaves block 70 percent of the incident solar radiation.

In West Africa, some of the larger loranths have become real pests. *Tapinanthus bangwensis* uses a wide variety of hosts but has become invasive in plantations since cocoa was introduced as a crop in the 1870s. It has been shown that germination of seeds and establishment of seedlings of this light-dependent parasite are up to three times more likely in unshaded compared to shaded cocoa trees. Therefore, the problem increased with deforestation and the practice of growing cocoa without shade trees. *Phragmanthera capitata* has invaded plantations of teak and rubber, and the presence of other large species of *Tapinanthus*, *Agelanthus*, and *Globimetula* only worsens the situation.

For many years, the only method to control attacks by members of Loranthaceae was cutting down these stem parasites. Some of the host branches must also be cut due to the spreading endophyte inside the branches and to prevent regeneration from secondary haustoria placed on so-called epicortical roots (Fig. 1). Otherwise, new shoots may arise from the endophyte or the adhesive disk. In recent years, herbicides have been tried, but very few herbicides are available for a system where both host and pest are dicotyledons. The substance 2,4-D dichlorophenoxyacetic acid has been sprayed onto the leaves of various members of Loranthaceae and Viscaceae or injected into the trunk of the host, but with inconsistent results. Herbicides may be used to control *Dendrophthoe falcata* on teak if used during the deciduous stage of the host tree.

Viscaceae

All members of Viscaceae are hemiparasitic stem parasites. The distribution is similar to Loranthaceae but with more species in the northern temperate zone. Only a primary haustorium is present, and the most advanced genera have a widely distributed endophyte. The flowers are small and inconspicuous, and the fruits are dispersed by birds except in the case of *Arceuthobium*, which relies on self-dispersal by explosive fruits. *Arceuthobium* species are the most harmful parasites on conifers in North America, but the maximum dispersal distance is 20 m from the mother plant, and long-distance dispersal rarely occurs. Although present in Washington State and British Columbia, no *Arceuthobium* has spread to any of the minor west coast islands. A population on Mt. Constitution, Orcas Island, is interpreted as an Ice Age relict. There are seven genera, but only *Viscum album* occurs as introduced.

Around the year 1900, the European *Viscum album* ssp. *album* (Fig. 2) appeared in Sonoma County north of San Francisco, California, not spread by birds but introduced by the highly respected plant breeder Luther Burbank. By 1984, the parasite had spread by birds to about 114 km^2. The average distance of spread from the point of introduction was 5.8 km. In 1991 the corresponding figures were 184 km^2 and 8 km. *Viscum album* ssp. *album* occurs on more than a hundred different hosts of broad-leaved trees,

FIGURE 2 *Viscum album* ssp. *album* on apple tree, March. The European mistletoe is introduced and invasive in California. Female plant with ripe fruits, seven years after sowing. (Photograph courtesy of the author. Reproduced from www.viscum.dk/abstracts/text/snylteplanter.pdf.)

and in California it has at least 22 hosts. Many of those are introduced species from Europe, but native North American species are also attacked, such as *Acer saccharinum*, *Robinia pseudoacacia*, *Alnus rubra*, *Populus fremontii*, and *Salix lasiandra*. Because mainly ornamental trees in urban areas are attacked, damage is considered moderate. Further spread is expected to be limited due to the presence of few acceptable hosts in the surrounding area. However, if spread by humans to gardens at long distances from Sonoma County, the parasite could be a real pest. *Viscum album* was recently also reported in Victoria, Canada. As for loranths, the control method is cutting off host branches. The cut must be at least 30 cm below the haustorium to ensure removal of all endophyte tissue.

Santalaceae

The sandalwood family, with 35 genera, consists of both woody and herbaceous species, which, with a few exceptions, are hemiparasitic root parasites. Here, too, the fruits are dispersed by birds. The family is represented in all climatic zones except the arctic zone. The mainly African *Thesium* is by far the largest genus, with about 250 species. The small, white-flowered, Eurasian *T. arvense* is reported near Calgary in Canada and in Montana and North Dakota in the United States. It most likely arrived with seeds of agricultural plants. The root parasite is mainly a grassland species that can attack vegetables, but due to its sporadic occurrence, it is not a threatening invasive species.

Cuscuta (Convolvulaceae)

Cuscuta (dodder) is the only parasitic genus in Convolvulaceae. It has a worldwide distribution and is absent only in the most northern parts of the northern hemisphere. There are at least 150 species (and possibly more), but there are many unsolved taxonomic problems. All species are herbaceous, winding, stem parasites with only secondary haustoria. Host range is high for most species but often difficult to determine, because *Cuscuta* haustoria attach to any subject within reach. However, many haustoria develop only a holdfast and no intrusive organ or endophyte. In such cases, the supportive species is not counted as a host.

Cuscuta species are fast growing (Fig. 3). This may in part be explained by faster nutrient translocation because the xylem bridge is accompanied by phloem. The presence of both xylem and phloem continuity is a unique feature in *Cuscuta*, and only one species of *Orobanche* is reported to have a similar advanced haustorium. *Cuscuta* species are annuals, and this life form, along with the fast growth, makes several species serious invasive weeds in agriculture, where crops such as tomato, potato, carrot, sugar beet, alfalfa, clover, avocado, coffee, and citrus species are attacked. The seeds are less than a millimeter in size. Very little is known about seed dispersal, but both birds and wind may be dispersal vectors. It is known that seeds survive the passage of the digestive canal of sheep. However, introduced invasive *Cuscuta* species probably always originate from contaminated seeds of crop plants. The invasive species causing most problems in many countries is the North American *C. campestris* (Fig. 3). In Asian countries, yield loss in sugar beet crops has been on the order of 3,500 to 4,000 kg/ha. In addition, *Cuscuta* may also be toxic to some domestic animals. No fully effective control method seems available. Mechanical methods such as flaming, harrowing, and hand-pulling

FIGURE 3 *Cuscuta veatchii* on *Bursera* sp., Baja California. The species is native, but its habit looks like the American *C. campestris*, which is invasive in many countries. The fast development of *Cuscuta* is illustrated by the fact that germination of the pictured species took place less than three weeks before this photograph was taken. (Reproduced from H. S. Heide-Jørgensen, 2008.)

have been used, and selective herbicides are also available but do not give full seasonal control. In 2004 the Asian *C. japonica* was discovered in California, and by 2007 it had appeared in 14 counties, indicating very fast dispersal. Furthermore, the growth rate is about 15 cm/day, and the host range is very wide. This indicates that *C. japonica* may soon be a troublesome invasive species.

Orobanchaceae

The broomrape family now includes witchweeds and other parasitic figworts. Of the about 90 genera, 75, representing 1,700 species, are hemiparasitic root parasites transferred from Scrophulariaceae. Furthermore, the family includes 17 genera of holoparasitic root parasites. The family is represented in all climatic zones and on all continents except Antarctica. Orobanchaceae contains the most troublesome introduced invasive parasites.

Parentucellia viscosa (Fig. 4) and *P. latifolia* from the Mediterranean region are annual root parasites in moist pastures and on heath land. Like other hemiparasitic root parasites, they have a wide host range, which includes native species in countries where they are introduced. They spread by tiny seeds carried by wind and water. *P. viscosa* occurs as introduced around the world in places such as Hawaii, the west coast of North America, Texas, Kansas, Denmark (where it is not a problem species), Japan, and Western Australia, and it is spreading further into Australia. Both species have recently been observed in the South Gippslands east of Melbourne. They can be fairly invasive and can degrade pastures if left unattended, but they may be controlled by use of selective herbicides.

FIGURE 4 *Parentucellia viscosa* introduced to Hawaii, the mainland United States, and many other countries. (Photograph courtesy of Forest and Kim Starr. Reproduced from H.S. Heide-Jørgensen, 2008.)

FIGURE 5 *Striga asiatica* on partly wilted sorghum. This is an invasive species in the United States and Australia causing serious losses in crops from the grass family. (Photograph courtesy of Arne Larsen. Reproduced from H.S. Heide-Jørgensen, 2008.)

Striga is another annual root parasitic genus. Seven of the 40 species are considered to be among the most damaging weeds within their mainly tropical African–Asian distribution. *Striga* is most common in semidry vegetation, where most species use grasses or sedges as hosts. In crop plants, *Striga* and *Orobanche* have found well-nourished, abundant hosts, allowing the parasites to develop extremely well and set lots of seeds. Therefore, these parasites become real pests, whether occurring as natural or introduced species. Two harmful *Striga* species, *S. asiatica* and *S. gesnerioides*, are known to be invasive in several countries. Long-distance dispersal is by wind or by insufficiently rinsed seed corn. Short-distance dispersal also occurs through water and by seeds sticking to claws, hoofs, footwear, wheels, and machinery.

S. asiatica (Fig. 5) was introduced into North and South Carolina, where it appeared in the 1950s, and into Southeast Australia. It is a serious threat in fields of maize, sorghum, and sugar cane. *S. gesneroides* was introduced into Florida. It mostly uses dicotyledons as its host—in particular, legumes. The seed set of *Striga* is on the order of 100,000 per plant, and the primary haustorium is so effective that by the time the parasite is visible above ground, it is too late to save the crop. In the most severe attacks, the yield loss may be up to 100 percent.

The large number of tiny seeds and a viability of more than 20 years are major problems for effective control of *Striga*. The most effective control is the development of resistant crop strains, and some success has been achieved in several crop plants. However, there are a number of methods, both mechanical and chemical, to avoid seed set, seed dispersal, and germination. These includes deep plowing to bury parasite seeds, hand-pulling, burning, cleaning tools and shoes, covering the soil with polyethylene to increase temperature, fallowing, fertilizing the soil, crop rotation, intercropping with catch crops, sowing early ripening strains late, practicing biological control using fungi and herbivorous insects, using chemical germination stimulants before sowing, fumigating soil with methyl bromide (for example), and using herbicides. None of these methods are effective or practical when used alone; it is necessary to use several of the methods simultaneously or successively as an integrated control system. It may also be noted that the biochemical and biological control methods are so expensive that they are not feasible in developing countries.

Orobanche is the largest genus in the family, with about 150 species (including *Phelipanche*). These are holoparasitic root parasites and mostly annuals. The root system is highly reduced, and several species have only a primary haustorium (Fig. 6). Seed production is enormous (up to 350,000 per plant). Dispersal biology is similar to that of *Striga*. At least six species are as problematic in agriculture as the harmful *Striga* species. They attack only dicotyledonous crops: mainly legumes (Fabaceae), but also others such as tomato, carrot, tobacco, hemp, and sunflower. The Mediterranean *O. minor* and *Phelipanche ramosa* (*O. ramosa*) have been introduced into several countries—*O. minor* into the United States, Chile, southern Africa, Australia, and New Zealand, and *P. ramosa* into Mexico, Cuba, Australia, New Zealand, and several U.S. states (it arrived in Texas as recently as 2000). The control methods and problems are the same as mentioned for *Striga*. In addition, soil application of an inhibitor of gibberellin synthesis prevents seed germination. *Orobanche amethystea* has recently been introduced to Israel, where it is invasive in vetch fields. Interestingly, introduced *Orobanche* species may be used to control other introduced species. *Orobanche flava* (Fig. 7) is introduced into Denmark, where it locally takes a heavy toll on the introduced and invasive *Petasites hybridus*.

FIGURE 6 *Orobanche hederae* on roots ("white") of ivy, *Hedera helix*. From the primary haustorium (center), a tubercle develops. Three inflorescences with chlorophyll-free, scaly leaves rise from inside the tubercle, along with a number of very short adventitious roots. Note that the host root has wilted beyond the primary haustorium, indicating very effective water and nutrient absorption by the parasite. (Reproduced from H. S. Heide-Jørgensen, 2008.)

FIGURE 7 *Orobanche flava* on *Petasites hybridus* (large leaves). Both species are introduced to Denmark. (Photograph courtesy of the author. Reproduced from www.viscum.dk/abstracts/text/snylteplanter.pdf.)

OTHER TAXA

More introduced parasitic species than mentioned above are known, mainly from Australia and New Zealand. Most of the species are annual hemiparasitic root parasites that are not yet considered invasive. *Cassytha filiformis* (Lauraceae) is a still-spreading stem parasite with a similar potential to be invasive as *Cuscuta*. As a curiosity, it may be mentioned that *Euphrasia frigida* (Orobanchaceae) arrived in 2000 as the first parasitic plant on the volcanic island Surtsey, formed 33 km south of Iceland after an eruption in 1963.

SEE ALSO THE FOLLOWING ARTICLES

Dispersal Ability, Plant / Forestry and Agroforestry / Horticulture / Invasion Economics / Seed Ecology / Weeds

FURTHER READING

Heide-Jørgensen, H.S. 2008. *Parasitic Flowering Plants.* Leiden: Brill.

Joel, D.M., J. Hershenhorn, H. Eizenberg, R. Aly, G. Ejeta, P. Rich, J. Ransom, J. Sauerborn, and D. Rubiales. 2007. Biology and management of weedy root parasites. *Horticultural Reviews* 33: 207–349.

Kuijt, J. 1969. *The Biology of Parasitic Flowering Plants.* Berkeley: University of California Press.

Mathiasen, R.L., D.L. Nickrent, D.C. Shaw, and D.M. Watson. 2008. Mistletoes: Pathology, systematics, ecology, and management. *Plant Disease* 92: 988–1006.

Press, M.C., and J.D. Graves. 1995. *Parasitic Plants.* London: Chapman and Hall.

Press, M.C., and G.K. Phoenix. 2005. Impacts of parasitic plants on natural communities. *New Phytologist* 166: 737–751.

Sand, P.F., R.E. Eplee, and R.G. Westbrooks, eds. 1990. Witchweed research and control in the United States. *Weed Science Society of America Monograph* 5: 1–154.

PATHOGENS, ANIMAL

GRAHAM J. HICKLING

University of Tennessee, Knoxville

Animal pathogens are disease-causing agents of wild and domestic animal species, at times including humans. In the context of invasion biology, the term usually refers to infectious microorganisms such as bacteria and viruses and excludes nonliving agents such as toxins and toxicants. These infectious organisms are sometimes termed *microparasites* to distinguish them from *macroparasites*. Introduction of new pathogens into areas occupied by susceptible animal host species threatens native wildlife, disrupts animal-based food production systems, and puts human and companion animal health at risk.

INVASIVE ANIMAL PATHOGENS AND EMERGING INFECTIOUS DISEASES

Pathogens are a natural component of all ecosystems. Long-term association with their vertebrate hosts results in coevolutionary responses that reduce the virulence of the pathogens or boost the ability of the host to resist or recover from infection. Human-induced changes to the environment disrupt these natural pathogen–host relationships, often with adverse consequences. A disease agent transported to a new area may trigger outbreaks of disease among hosts previously naive to that pathogen—the introduction of rinderpest virus to Africa in the 1880s provides a grim example. Changes in transmission pathways of endemic pathogens can trigger unanticipated epizootics, such as when the 1827 introduction of *Culex quinquefaesciatus* mosquitoes triggered outbreaks of avian pox among birds on the Hawaiian Islands; the pox virus was already present on the islands but had not previously been causing significant disease. Change in habitat or climate can alter the biogeographic distribution of the vectors and hosts of animal pathogens, leading to disease invasion (or reinvasion of areas previous cleared of that disease). Collectively, these kinds of outbreak are termed emerging infectious diseases (EIDs), defined as infections that have newly appeared in a population or that are rapidly increasing in incidence or geographic range (see Table 1 for examples of EIDs affecting animals). The majority of EIDs affecting humans originate from pathogens originally carried by other animal species; these diseases are termed zoonoses. Examples of zoonoses include some strains of avian influenza, and flaviviruses such as West Nile virus.

FACTORS RESPONSIBLE FOR ANIMAL PATHOGEN INTRODUCTION AND INVASION

Increased frequency and speed of local and international travel, increased human-assisted movement of animals and animal products, and changing agricultural practices have all favored the introduction of animal pathogens to new areas. Genetic and environmental changes also facilitate animal pathogen invasion.

Changes in the Genetic Make-up of Pathogens

Animal pathogens sometimes become invasive as a consequence of natural changes in their genetic make-up, producing new strains with increased transmission rates or pathogenicity. For example, a new calicivirus closely related to the virus responsible for European brown hare syndrome emerged in rabbits in China in 1984 and spread to other countries via trade in farmed rabbits. The resulting outbreaks of rabbit hemorrhagic disease were highly lethal to unvaccinated European rabbits.

Humans, animals, and environmental sites are all reservoirs of bacterial communities that include some bacteria resistant to common antimicrobial agents. Our agricultural practices are increasingly providing environments in which these resistant bacteria can amplify and spread, so there is growing concern that enhanced microbial resistance will lead to future pathogen outbreaks. Nevertheless, most animal pathogen introductions are triggered by the movement of humans and other animals, or are a consequence of human-induced environmental change.