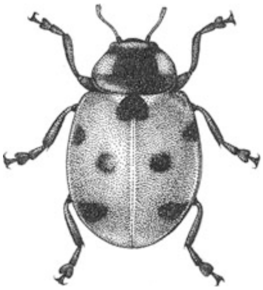

Fig. 3.3 *Coccinella septempunctata* Linnaeus 1758 (seven-spotted ladybird beetle)

3.3 Biodiversity

The term **biodiversity** means "the diversity of life" and includes:

- the diversity within a species or population (**genetic diversity**; see also Box 2.1),
- the number of species within a defined area or within a spatial or functional subunit of a community (**species diversity**), and
- the different components or habitats of a landscape (**landscape diversity**).

3.3.1 Species Diversity in Natural Systems

The number of species in an area or in a community is determined not only by the ecological conditions of the site but also by geographic factors. Viewed from a global perspective, the natural species diversity is very unevenly distributed. In principle, an increase in species diversity from the poles to the equator is evident and true for various groups of organisms, for example trees, mammals, birds, reptiles, and different orders or families of insects, for example ants (Table 3.1).

Tropical rain forests can have far more than 100 tree species per hectare, whereas in forests of the temperate latitudes a maximum of 30 species (North America) or 15 species (Central Europe) can usually be found per hectare. In a boreal forest, a maximum of five tree species is found in the same area. An additional gradient in biodiversity exists in mountainous regions, where the number of species decreases with increasing altitude.

Worldwide, the most diverse ecosystems, which primarily include rain forests and coral reefs, are found in the tropics.

The causal relationships between species diversity and latitude or altitude are unclear. However, it may be assumed they are primarily based on climate factors.

Table 3.1 Numbers of ant species found at different geographic latitudes of the Americas and Europe

Region	Latitude	Number of ant species
America		
Alaska (arctic part)	65–70° N	3
Alaska (total)	58–70° N	7
Iowa, USA	41–43° N	73
Utah, USA	37–42° N	63
Cuba	20–23° N	101
Trinidad	10–11° N	134
São Paulo, Brazil	20–25° S	222
Missiones, Argentina	26–28° S	191
Tucuman, Argentina	26–28° S	139
Buenos Aires, Argentina	33–39° S	103
Patagonia (total)	39–52° S	59
Patagonia (western part)	40–52° S	19
Tierra del Fuego	53–55° S	2
Europe		
Norway (northern part)	>69° N	10
Norway (total)	58–70° N	34
Germany	47–55° N	62
Italy	34–47° N	104

Based on Kusnezov (1957)

These are essentially related to incoming solar radiation (light and heat) and water supply (quantity and distribution of precipitation). These factors are also involved in the distribution of species at small scales (e.g. within a landscape) and are affected by, for example, the topography and exposure of a site.

Another factor that determines the species diversity of a habitat is the availability of food resources (for animals) and the availability of nutrient resources (for plants). However, the number of plant species is not highest on sites with the highest nutrient availability, but generally declines with increasing soil nutrient content. In cultivated landscapes also, it can be observed that highly nutrient-rich sites usually have low species diversity. For example, the edges of moving waters are usually well-supplied with nutrients, because of flooding, yet plant stands are usually species-poor and, in Central Europe, often dominated by one species only, for example the stinging nettle (*Urtica dioica*) or the common butterbur (*Petasites hybridus*). In contrast, nutrient-poor habitats, for example marginal grasslands, are often particularly rich in plant species. These situations occur primarily because only a few plant species can actually efficiently utilize high nutrient quantities. Such species have a growth and competitive advantage over most species, which are adapted to relatively nutrient-poor conditions.

There are usually close connections between the number of animal and plant species in a habitat. The more plants species found at a site, the more phytophagous species can exist there, because most of these are feeding specialists (Sect. 4.5.2). This, in turn, increases the number of potential prey species for predators with diverse food requirements. Species-rich plant stands also have greater structural diversity than species-poor plant stands, which also increases the range of potential ecological niches for various organisms.

3.3.2 *Agricultural Biodiversity*

The main aspects of biodiversity of agroecosystems include the diversity of the varieties and breeds of domesticated plant and animal species, and the natural diversity of species related to crop production (wild plants, pollinators, pests, and their natural enemies). This is in addition to the relationships between agroecosystems and their surrounding species, habitats, and ecosystems at the landscape scale.

3.3.2.1 Genetic Diversity of Crop and Livestock Species

Approximately 7,000 species of plants have been cultivated since humans started arable farming. Currently, only approximately 30 crops provide 95% of human food energy needs; four of these (rice, wheat, maize and potato) are responsible for more than 60% of our energy intake (FAO 2012).

In addition, the genetic diversity of these crop species has dramatically decreased. Of 8,000 traditional rice varieties grown in China in 1949, only 50 remained in 1970. In 1950, India had 30,000 wild varieties of rice, but in the near future, only 50 are expected to remain. Mexico has lost an estimated 80% of its maize varieties (Fowler and Mooney 1990). Overall, it is estimated that 75% of the genetic diversity of crop plants was lost in the twentieth century (FAO 1997). The main reasons for this development were the introduction of high-yielding varieties after the Green Revolution (Sect. 8.1.2.2) and the overall intensification and homogenization of crop production. This resulted in a change of traditional farming practices in which a large number of different, often locally-adapted, landraces of different genotypes were planted in the same field or on the same farm.

Of the estimated 15,000 species of mammals and birds, only between 30 and 40 have been domesticated for food production and fewer than 14 species, including cattle, goat, sheep, buffalo, and chicken, account for 90% of global livestock production. Of the total of about 7,600 livestock breeds, approximately 20% are classified as at risk of extinction. The rate of extinction amounts to almost one breed per month. Similar to the losses in crop diversity, the reason for this development is the intensification of production, utilizing a narrow range of breeds. Global production of meat, milk, and eggs is increasingly based on a limited number of high-output breeds—those that are most profitably utilized in industrial production systems (FAO 2007).

Global reductions in crop and livestock genetic diversity have a variety of implications for food production and security in the future:

- Reducing the genetic diversity of crops and livestock renders them more vulnerable to pests and diseases, which are more likely to spread when varieties or breeds have a similar genetic base. Although genetic uniformity itself does not necessarily mean higher vulnerability, it increases the likelihood that a pest or disease could affect a great proportion of the cropping area or livestock herd compared with the simultaneous use of a greater number of genotypes, which reduces the probability of large-scale epidemics. For example, genetic uniformity contributed to the spread of the Southern corn leaf blight (*Bipolaris maydis*), a fungus disease which led to a 15% reduction in the US corn yield in 1970.
- Similarly, genetic uniformity can increase vulnerability to abiotic stresses. This becomes increasingly important in the face of global climate change with expected changes in temperature, rainfall patterns, and an overall increase in the likelihood of extreme weather, for example droughts, heavy precipitation, and heat waves (Sect. 8.1.3). Genetic variability within a species confers at least the potential to resist stress, in both the short and long term. Therefore, the variance in yields from a more diverse crop system will be less than for a system with only one variety. In addition, crop genetic diversity is of particular importance to marginal sites and regions, which are less suitable for growing high-yielding varieties.
- Plant genetic resources present in traditional landraces or their wild relatives constitute an important basis of plant breeding. Diversity in plant genetic resources provides plant breeders with options to develop new and improved varieties. These are adapted to specific abiotic conditions or have such desired characteristics as resistance to diseases and pests.

For such reasons, genetic resources are required as inputs into the continuing process of enhancement through selective breeding (including genetic engineering). In the face of rapid global changes in climate and land use, conservation of crop and livestock genetic resources becomes increasingly urgent and requires the collection, evaluation, and deployment of such genetic material.

In general, genetic resources can be conserved either **in situ** (in their natural setting or in the field) or **ex situ** (outside their natural setting in gene banks). Gene banks are based on collections of genetic material (especially seeds) mainly from centres of crop origin, that are stored under controlled conditions and periodically regenerated (planted and grown) to maintain seed viability. However, not all kinds of plant genetic resource can be easily conserved ex situ and must, therefore, be kept as living plants in situ, which is more costly and requires additional land and labour.

There are approximately 1,400 gene banks around the world that contain approximately six million accessions (samples) including landraces and wild relatives of domesticated crops. Most of the genetic material has been collected from the world's major crops (rice, wheat, and maize). It is estimated that more than

90% of the genetic diversity of these crops is preserved ex situ. However, most of the minor crops, especially those which are of local importance only, are poorly represented or are in no genetic collections.

3.3.2.2 Species Diversity in Cultivated Landscapes

Before the start of the first agricultural activity approximately 7,000 years ago, Central Europe was almost completely covered with forest. Clearing of the forest led to the creation of open sites (mostly arable fields and meadows) that differed from the forest primarily in the solar radiation that reached the ground and, therefore, in light and temperature conditions. Thus, habitats developed for plant and animal species that previously only occurred in warmer and woodless regions, especially the Mediterranean region and the grasslands of southeastern Europe and western Asia. Such species could spread from their original ranges and colonize the new open habitats. Animal and plant species that profit from human modifications of the environment, especially the creation of cultivated systems, are termed **hemerophiles** (Greek *hemeros* = cultivated and *philos* = friend). Meanwhile, forests continued to exist alongside the cultivated areas. Therefore, the landscape of Central Europe today has significantly greater species diversity than it did before interference by humans.

In addition to crop species and varieties, of which usually only one or a few are cultivated in a single field, other factors determine the biodiversity of agroecosystems and cultivated landscapes. These include

- geographic, climatic, and soil conditions;
- type and intensity of cultivation; and
- diversity, structure, size, and distribution of habitats in the landscape.

Since the introduction of agriculture, the number of wild plant species in agroecosystems in Central Europe has steadily increased (Fig. 3.4). In a similar way, the number of animal species living there has probably also increased.

However, in the second half of the twentieth century, a substantial decline in the species diversity of agroecosystems occurred, primarily among wild plant species on many sites. Their decline has amounted to 50% on average. The loss of biodiversity not only affects agroecosystems, but also the diversity of cultural landscapes and their resident species, which include birds and such mammals as the European hare (*Lepus europaeus*). The cause is the increasing intensification of agricultural production, in which the following practices are of importance:

- Structural changes in the agricultural landscape. These are primarily the result of enlargement of field size, which is often accompanied by removal of bordering landscape elements (e.g. field breaks, hedgerows, stone walls) which serve as habitats and refuges for many animal and plant species. In addition, an increase in planting density (especially for cereals) and a decline in the diversity of

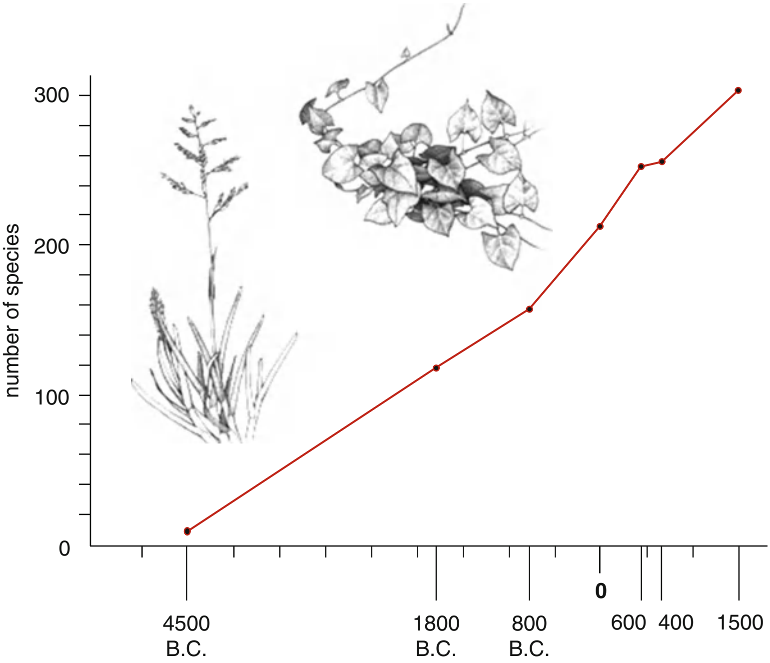

Fig. 3.4 Number of weed species recorded in Central Europe between the Mesolithic and Middle Ages (Based on Willerding 1986). As examples, the illustrations show annual meadow grass (*Poa annua*; *left*) and wild buckwheat (*Fallopia convolvulus*; *right*).

cultivated crop species has occurred, which further impairs chances of survival for many plant and animal species in the fields.

- Increased application of fertilizers. As in natural sites, the number of wild plant species in fields and grasslands is lower on sites with high nutrient supply (especially nitrogen) than on unfertilized control sites (Fig. 3.5a). In contrast, biomass production by the plants is higher on fertilized sites than on unfertilized sites (Fig. 3.5b).
- Weed and pest management. Not only herbicides (Sect. 5.1.1) but also other methods of weed management led to a decline in the diversity of wild plant species. Some of these species are highly dependent on dispersal via crop seeds, in which their seeds are stored with the harvest of the crop species and distributed back on to the fields with the next sowing. This pathway has been strongly limited by modern methods of seed cleaning. Therefore, species such as the common corn cockle (*Agrostemma githago*), have become very rare in the agricultural landscapes of Central Europe. Indirectly, many animal species are also affected by weed management because a decline in wild plant species results in a decline in resources. Insecticides (Sect. 5.2.1) affect not only pests but also other species of agricultural habitats, and therefore reduce species diversity overall.

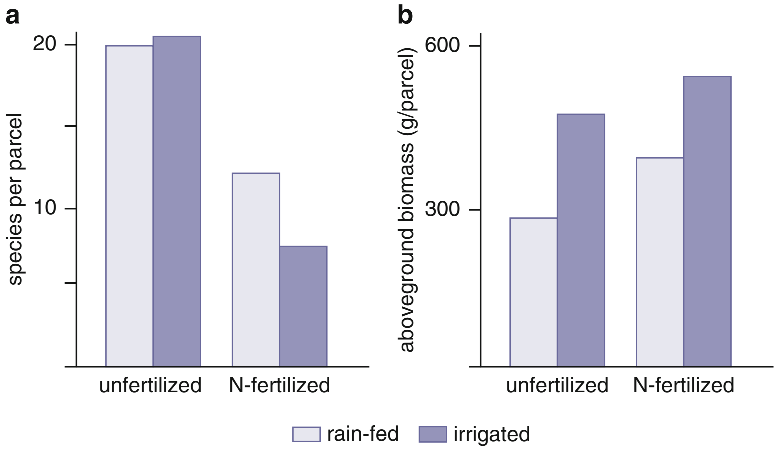

Fig. 3.5 Effects of nitrogen fertilization on (**a**) the number of plant species and (**b**) the aboveground biomass of irrigated and rain-fed parcels of 1-year fallow land in Michigan, USA (Based on Goldberg and Miller 1990)

- Grazing and mowing of grasslands. In addition to fertilization and weed management, plant species diversity of meadows and pastures is affected by mowing or grazing. Livestock species, for example cattle and sheep, can modify the vegetation of grasslands in different ways. At low stock density, they often maintain or increase the number of plant species, but high livestock densities can reduce diversity. These effects result from modification of the competitive relationships between plants—selective grazing of dominant grass species improves conditions for formerly suppressed species but high grazing pressure can eliminate sensitive species. In addition, diversity is affected on small scales by urine and faeces deposition and by trampling, affecting plants directly or indirectly via soil compaction. Furthermore, large-scale overgrazing can lead to different forms of land degradation (details are given in Sect. 6.2.1).

Paradoxically, modern agriculture is partially responsible for the decline in species whose presence in Central Europe was made possible only by the establishment of agroecosystems.

With reductions in plant and animal diversity, intensification of agroecosystems also affects the **functional biodiversity** of a system. Generally, functional biodiversity refers to the different types of species interactions and food web structures which are related to different processes including productivity, yield and other properties of the agroecosystem. Important aspects are further discussed in other chapters and include interactions between pests and their antagonists in the context of biological pest control (Sect. 5.2.4), pollinator services (Sect. 4.5.3), and invasive species (Sect. 3.3.3).

Anthropogenic modifications of ecosystems and agroecosystems can change the distribution ranges of species. This not only includes expansion of species' range, as occurred for many species after the introduction of agriculture to Central Europe, but can also limit the range, which can lead to the complete disappearance of species. Globally, changes in species diversity are determined by two processes only: the evolutionary emergence of new species, which can take millions of years, and the extinction of species. The latter is currently occurring, with estimates ranging from 17,000 to 100,000 species lost per year. A substantial part of the reason for this decline in species is the creation of agricultural land.

The cultural landscapes of the humid tropics are in extreme contrast with the Central European cultural landscape, which developed over the course of thousands of years. With the exception of some regional examples, tropical cultural landscapes are young, most of which were created in the twentieth century by removal of forest. Because tropical forests are among the most biodiverse ecosystems on Earth, their destruction is accompanied by substantially higher losses of biodiversity than is the case with the forests of Central Europe. On agricultural sites in the humid tropics, which are no longer suitable for agricultural use because of nutrient depletion, forests generally do not re-establish. Instead, extremely species-poor vegetation develops, which is dominated by species such as the grasses *Imperata cylindrica* and *Saccharum spontaneum* or bracken (*Pteridium aquilinum*). These plants are literally "cosmopolitan" and are found on all continents. Nature protection, as conducted in Central Europe to maintain the species of the cultural landscape, is superfluous in such regions. Appropriate measures in the tropics must concentrate on the conservation and regeneration of forests.

3.3.3 Invasive Species

As pointed out above, the global expansion of agriculture has led to shifts in the distribution and range expansion of many plant and animal species. This process started with many of the cultivated crops which have been actively introduced to new regions of the world. Further human activity, especially the expansion and intensification of global trade, resulted in the (largely accidental) exchange of different species between regions and continents. Worldwide, numbers of introduced wild terrestrial, freshwater, and coastal marine animal and plant species are continuously increasing (Fig. 3.6).

Overall, species that have reached regions where they did not previously occur as native species, are termed **alien species** or **exotics** in their new environment. The occurrence of most of these species is limited to small plots or areas where they have become established. A special category of exotics, however, are species which are able to expand their populations by invading new habitats. By this means they have negative effects on native species, communities, or ecological processes in natural or agricultural systems. Species with such characteristics are called **invasive species**. Besides this ecological definition, an invasive species can be termed "*an*

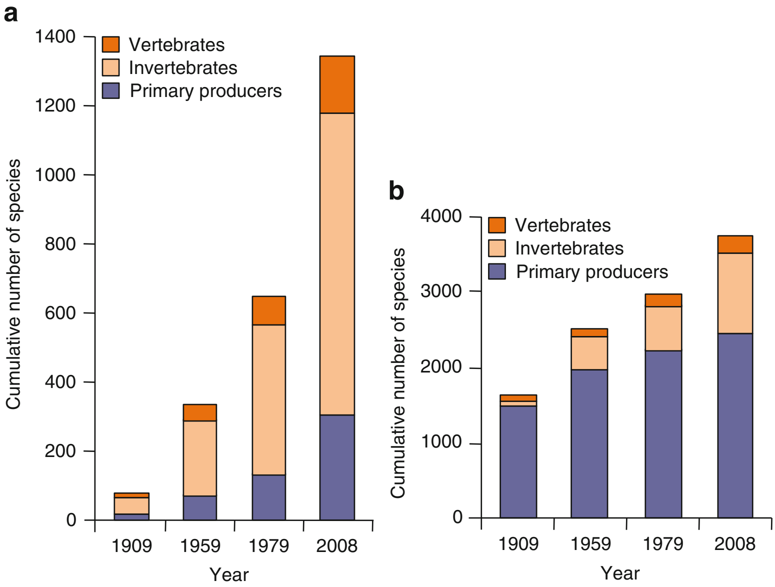

Fig. 3.6 Cumulative number of alien species established in (**a**) European marine/estuarine waters and (**b**) terrestrial environments in 11 European countries (Based on EEA 2010)

alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health" (Beck et al. 2008).

The list of the world's worst invasive species (ISSG 2012) includes animal and plant diseases (e.g. rinderpest virus and phytophthora root rot, *Phytophthora cinnamomi*) insects (including five ant species), other invertebrates (e.g. giant African snail, *Achatina fulica*), feral animals (e.g. rabbit, *Oryctolagus cuniculus*), and numerous species of plants, including algae, herbs, and trees.

3.3.3.1 Impact of Invasive Species

The spread of invasive plant and animal species is believed to be the largest threat to global species diversity, besides direct human effects on natural ecosystems. Biological invasions have contributed to the decline of 42% of the endangered and threatened species of the United States (Wilcove et al. 1998). In other parts of the world, 80% of the endangered species are threatened as a result of invasion by alien species (Pimentel et al. 2005). Oceanic islands suffer especially high rates of species decline and losses. Invasive rats (*Rattus* species) have been implicated in the extinction or decline of hundreds of island endemic vertebrates. Predation by the brown tree snake, (*Boiga irregularis*) introduced to the island of Guam, caused nearly complete extermination of the island's native forest birds. In many cases, the invaded species cause subsequent changes in the native communities by distorting

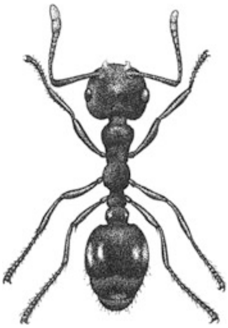

Fig. 3.7 Red fire ant (*Solenopsis invicta*)

food web interactions with cascade effects on many other species, or by changes in ecosystem structures and functions (e.g. of nutrient cycles, productivity, or habitat structure). Such modifications can facilitate the establishment of additional invasive species.

Further effects of invasive species related to land use and agricultural production are shown by the following examples:

- The red fire ant (*Solenopsis invicta*; Fig. 3.7) originates from South America and was inadvertently introduced to North America in the 1930s, where it rapidly spread throughout the southern United States.

More recently, the red fire ant was also introduced to Australia, China, and other regions. In the United States, the ants colonize open disturbed habitats including agricultural fields, rangeland, and gardens. Their colonies can reach 250,000 individuals. The species is omnivorous and acts as general predator and consumer of plant materials. As a predator, it affects all levels of species within the food chain, with effects on numerous invertebrates and ground-inhabiting vertebrates including birds, reptiles, and small mammals. They can reduce the species diversity of arthropod communities to 40% (Porter and Savignano 1990). Red fire ants are also reported to directly damage a variety of crops, for example tomato, corn, soybean, and sunflowers, by feeding on the seeds, seedlings, and developing fruits. Furthermore, red fire ants are very aggressive when disturbed and have a painful burning sting, which can cause allergic reactions. In addition to humans, fire ants also attack and harm large mammals, including wildlife, cattle, sheep, and horses on their grazing lands. Overall, the economic effect of fire ant infestations is enormous, with costs of control, medical treatment, and the various forms of damage running annually to several billion dollars in the United States.

- The aquatic golden apple snail (*Pomacea canaliculata*, Fig. 3.8) is native to tropical and subtropical South America where it lives in floodplains and seasonal wetlands. The snail is a polyphagous herbivore and feeds on floating and submersed higher plants. In the 1980s, it was introduced to Southeast Asia (first to Taiwan) with the purpose of establishing an additional source of food and income for farmers. The programme failed and, instead, the snails escaped

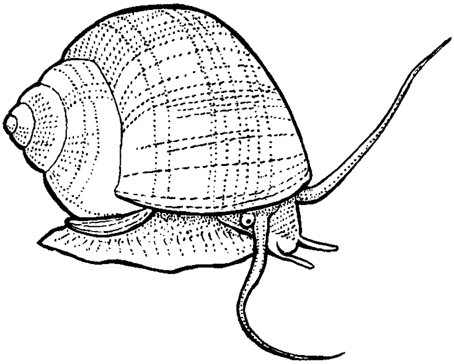

Fig. 3.8 Golden apple snail (*Pomacea canaliculata*)

and became dispersed to other countries, where they colonized irrigated rice fields. These provide a suitable habitat where the snails can also survive dry fallow seasons. Because wild aquatic plants are controlled by weed management in intensive rice production systems, *P. canaliculata* attacks young rice seedlings because of the lack of alternative food sources. Today, this invasive species occurs in nearly all rice-production areas of tropical and subtropical Asia and has developed into a major pest in rice production. The yield loss caused by *P. canaliculata* in rice has been estimated to vary from 5 to 100% depending on locality and population density.

- Kudzu (*Pueraria montana*) is a perennial leguminous vine (Fabaceae) native to East Asia (China, Japan, Korea). The plant was introduced to the United States in the late nineteenth century for a variety of purposes: it was used as an ornamental plant, as fodder plant for cattle, and as a cover plant to prevent soil erosion. In the southeastern United States, the plants escaped control and became distributed on different types of open land. Preferred habitats are forest edges, abandoned fields, and shrubland. Kudzu grows rapidly and is able to cover and smother orchards and plantation crops, including young forest plantations, and leads to the dieback of the overgrown vegetation. This reduces diversity and causes economic loss, especially in forestry.
- Invasive weeds are major threats to the biodiversity and livestock production of rangelands across large parts of the world. In the western United States, rangelands previously dominated by perennial bunchgrasses have been converted, primarily as a result of overgrazing, to annual grasslands that are susceptible to invasion by introduced dicots. According to DiTomaso (2000), there are more than 300 rangeland weeds in the United States. Some of the most problematic species include at least 15 species of the genus *Centaurea* (Asteraceae, knapweeds), for example *Centaurea diffusa* (Fig. 3.9). These and other weed species are low in palatability and avoided by livestock, and some are actually poisonous to livestock. Overall, they reduce the quality of forage, increase the cost of managing and producing livestock, slow animal weight gain, and reduce the quality of livestock products. Furthermore, many rangeland weeds have deep taproot systems which modify the water balance and nutrient availability of the system.

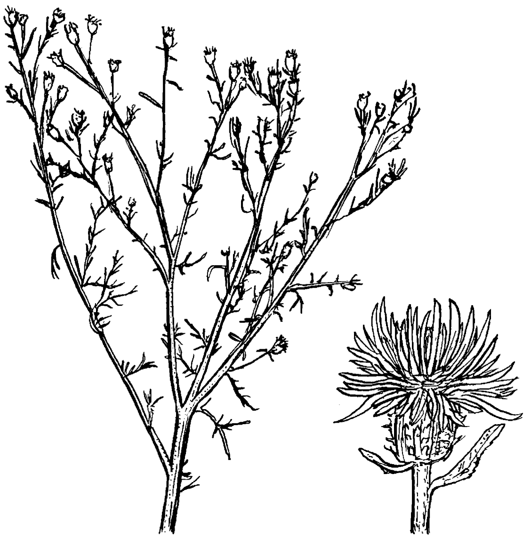

Fig. 3.9 Diffuse knapweed (*Centaurea diffusa*)

In Australia, up to 2,000 alien wild plant species became naturalized by the end of the twentieth century, with an estimated continuing rate of increase averaging 10 species per year. Many are weeds of rangelands, including such invasive shrubs as *Parkinsonia aculeata*, *Mimosa pigra*, *Acacia nilotica*, and *Prosopis* species. There is also concern that alien plant species include "sleeper weeds" that may become invasive and expand their range as a consequence of climate change.

The chances of controlling invasive species are usually limited. There are only a few examples of successful suppression of an invasive species, for example biological control of St. John's wort (*Hypericum perforatum*), an invasive rangeland weed of North America in the first half of the twentieth century (Sect. 5.2.4.7). However, complete eradication of an alien species can be achieved only during the very early stages of an invasion. Therefore, most attempts to control invasive species focus on measures to prevent their spread and impact. This requires detailed knowledge on the biology and ecology of the target species to develop an overall strategy which may cover a combination of management techniques including mechanical, chemical, and biological control and the control of invasive species transportation pathways.

3.3.3.2 What Makes Invasive Species So Successful?

Only a relatively small proportion of exotic species develop into invasive species in the region of introduction. For example, 21% of the North American flora consists of exotic species, but only 2% of these have developed to become pests (Doorduin and Vrieling 2011). Williamson (1996) proposed the "10:10 rule" to explain the probability of a species becoming a successful invader, meaning 10% of introduced species become established and 10% of those will become invasive.

As many as 29 individual mechanisms or processes have been proposed to explain why some alien species can achieve higher densities, higher rates of spread, and greater establishment success than others (Catford et al. 2009). Basically, these refer to (1) specific characteristics and traits of the invasive species and/or (2) characteristics of the invaded environment:

1. Biological traits of plants and animals that provide competitive advantage over native species and which are of advantage for successful invasion may include one or more of the following: (a) high rates and specific strategies of reproduction, (b) broad tolerance of temporarily unfavourable environmental conditions and disturbances, (c) high phenotypic plasticity, (d) the ability of adaptive evolution, (e) high resource use efficiency, and (f) effective (chemical) defence mechanisms against natural enemies.
2. Characteristics of the new environment consist of both abiotic and biotic factors that affect invasion success. These include (a) the overall climatic conditions and the available resources, (b) the presence and abundance of natural enemies, including diseases, (c) the ability of resident species in a community to reduce growth and performance of invading species populations (i.e. biotic resistance, which may depend on ecological interactions, food web structure, and species diversity of a native community), and (d) the amount of anthropogenic disturbance of vegetation, soil and other ecosystem characteristics and functions.

However, empirical evidence suggests that most of these species-specific and environmental factors can explain the success of some invaders only to some extent in some circumstances. Rather, invasion success is likely to be context-dependent and a result of a combination of different factors and mechanisms which can hardly be predicted for individual species. In addition, an initial determinant of invasion success can be the number of individuals of the species introduced and the frequency of introductions. The different factors and potential pathways that can result in a successful species invasion are shown in Fig. 3.10.

3.4 Succession

The process of directed, continuous and season-independent changes in communities, which are accompanied by the colonization of new species and the disappearance of previously present species, is called **succession**. This process consists of the sequence of different communities which may occur over the course of short or long term periods (a few years to millennia) and is determined by biotic and abiotic factors. Examples include changes in the communities of abandoned fields, tree fall, clear-cuts and fires in forests, sand dunes, or the development of new sites created through landslides.

The endpoint of such a development, reached under the given climatic conditions of a site, is called the **climax community**. Examples of the climax stage of different climate zones include tundra, taiga, savanna, steppe, tropical rain

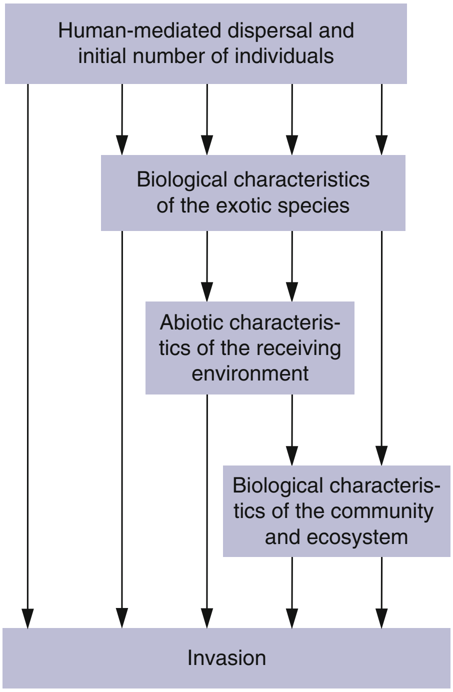

Fig. 3.10 Different factors and potential pathways that can result in a successful species invasion (Based on Catford et al. 2009)

forest, and deciduous forest in the temperate regions (Chap. 7). However, the climax community of individual sites within these climate zones can vary substantially in terms of species composition. This is determined primarily by abiotic site factors and interactions of the colonizing species.

Under nearly constant environmental conditions, the climax conditions are relatively stable, i.e., only short-term, undirected, and temporary fluctuations in the composition of the community occur. The causes of such **fluctuations** are, primarily, weather conditions, that can vary on a seasonal or yearly basis. Large changes in the species composition of climax communities occur only as a result of specific external effects or disturbances. For example, these can include changes in climate, the rise or fall of the water table, or inputs of nutrients. Depending on the effect of these factors, different developments may occur as a consequence.

Agroecosystems are stages of succession that do not undergo further development because of regular agricultural measures, for example sowing, harvest, and soil cultivation. This is observed for grasslands in regions of natural forest vegetation (for example the temperate regions of Europe) which only remain in this stage because of regular mowing or grazing. After abandonment of use, such systems undergo natural succession. On fallow fields in Central Europe, the following phases may be identified in such a succession:

1. In the beginning, annual wild plants dominate. These primarily include species that are found in cultivated landscapes as weeds (Sect. 4.4).

2. Next, perennial, herbaceous plants become established and gradually displace the annuals. Plant species diversity is highest in this phase.
3. In the third phase, woody plants begin to become established (shrub or bush phase). With increasing shade, the herbaceous species are displaced and the plant stand becomes more species poor.
4. In the final stage, trees are dominant and a closed forest develops.

The development of such a community can vary substantially in terms of species composition and the duration of different stages of development, depending on the site. Detailed predictions of the course of succession are therefore hardly possible. The development of agricultural fallow land is primarily determined by three groups of factors. These are:

- previous cultivation, the effect of which is largely determined by the last cultivated crops and agricultural practices, for example fertilization, soil cultivation, and use of herbicides. These factors significantly affect the growing conditions of the plants, and the seed bank found in the soil.
- natural site conditions, which are primarily determined by the climate, soil properties, the exposure, and slope. Generally, drier and cooler site conditions mean that succession proceeds more slowly.
- the vegetation in the direct and more distant vicinity of the site. The frequency of individual plant species, their distance from potential sites of colonization, and the dispersal ability of their seeds affect species composition, especially in early stages of succession. The presence of shrubs which spread through vegetative stolons can accelerate the encroachment of scrub on to fallow land.

Not only plant communities but also animal communities undergo succession. For example, flower-rich, herbaceous plant stands, which develop in the first years on agricultural fallow land are correlated with the presence of butterflies and wild bees. In addition, they provide resources for specific antagonists of pests of cultivated plants (Sect. 5.2.4.5).

The intentional establishment of agricultural fallow land, as a component of the cultural landscape, can contribute to conservation of the species diversity of typical field flora and fauna.

3.5 Flows of Energy and Material

Energy and organic and inorganic materials are continuously transported and transformed within the compartments of an ecosystem, and between different ecosystems. These processes are carried out by organisms and as a result of abiotic factors, for example water and wind.

Table 3.2 The ecological efficiencies which determine the portion of net primary productivity that is used by consumers for production of biomass within an ecosystem

Utilization efficiency in different ecosystems	
Forests	2–7%
Cropping systems[a]	9–21%
Grasslands	5–60%
Oceans	40–99%
Assimilation efficiency of different consumers	
Wood-eaters (xylophages)	15%
Grass and leaf-eaters (herbivores)	30–50%
Seed-eaters (granivores)	70–80%
Predators	70–90%
Detritivores	20–40%
Production efficiency of different consumers	
Mammals and birds	1–3%
Insects and other invertebrates	10–55%

Based on Whitaker (1975), Wiegert and Owen (1971), Humphreys (1979) and other sources

[a] Yield losses of the most important food crops worldwide attributed to phytophages (Based on Oerke et al. 1994)

3.5.1 Energy Flows Through Food Webs

The energy flows in ecosystems proceed via food chains and food webs. Of the total energy fixed by photosynthesis in a plant, representing **gross primary production (GPP)**, only a portion is converted into biomass, representing **net primary productivity (NPP)**. The difference between GPP and NPP is the portion of energy that is needed by the plant for the maintenance of metabolic processes; this is released as heat. Primary production is measured in grams of carbon (C) or grams of biomass (fresh or dry weight) per unit area per year.

The NPP of natural vegetation types on Earth varies within a broad range. In different terrestrial ecosystems, NPP can range from just a few g C m^{-2} year^{-1} in deserts to approximately 2,000 g C m^{-2} year^{-1} in tropical rain forests. The reasons for this are not only the differences in the yearly radiation received from the sun by the different latitudes on Earth (Sect. 4.1), but also such other factors as water and nutrient availability to plants. The proportion of NPP utilized in the production of biomass by the various organisms within the consumer food web is determined by different ecological efficiencies:

- The **utilization efficiency** is the proportion of NPP of a plant stand that is taken up by phytophagous consumers as food. This efficiency varies significantly among different ecosystems (Table 3.2). In a forest, this value is almost 7% (the differences between temperate and tropical latitudes is slight) and is primarily consumed by insects. In grassland ecosystems, utilization efficiencies range from 5 to 60%. The highest values for terrestrial ecosystems are found in the African savannas, for which grazing mammals are mostly responsible. Of the

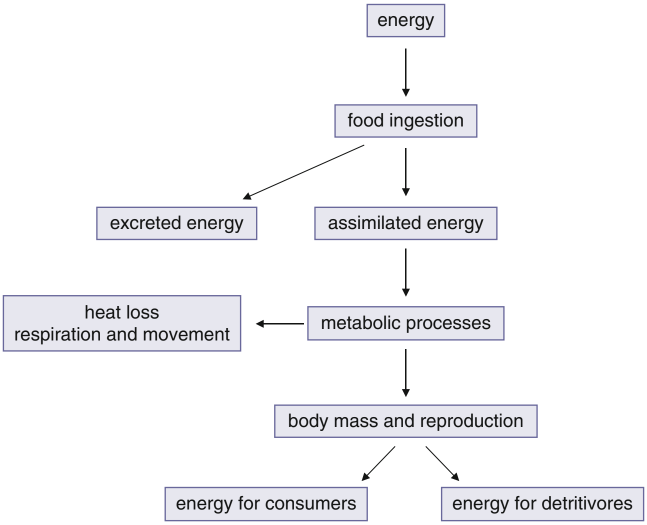

Fig. 3.11 Pathways of energy within a trophic level

globally most important crops in agroecosystems, between 9 and 21% are consumed by phytophagous pests.

- The **assimilation efficiency** represents the portion of the consumed biomass that is available to the consumer as energy source. Thus, it cannot be equated with the quantity of food that reaches the digestive system. Of this, a portion of variable size cannot be used by the organism and is therefore excreted. The assimilation efficiency depends on the quality of the food and the ability of the organism to make the food's energy content available during digestion (Table 3.2). In leaf and grass-eaters, the assimilation efficiency is approximately 30–50%, which means that at least half of the ingested food remains unused. Wood-eating species assimilate only approximately 15% of their food. The assimilation efficiency of seed and fruit-eaters and of secondary consumers (predators) is up to 80%. As in the producers, the assimilated energy is used primarily for two processes—respiration, in which it is released as heat, and production of biomass.
- The **production efficiency** is the proportion of assimilated energy that is available for production of biomass, i.e. for growth and reproduction. Groups of consumers can also be classified on the basis of this efficiency (Table 3.2). Mammals and birds, which must maintain a higher body temperature, can transform 1–2% of assimilated energy into biomass whereas insects and invertebrates can transform 10–55%.

The pathways of distribution of energy within a trophic level are shown in Fig. 3.11. The energy stored within the biomass of dead organisms provides the basis of the detritivore food web.

The energy that flows into the food web via the producers declines from one trophic level to the next. The related transfer efficiency varies with each ecosystem and the associated organisms.

3.5.2 Material Transport Through Water and Wind

In many landscapes, **water** is the most important transport medium for organic and inorganic material. Streams and rivers take up soil and detritus from their watershed. In flood plains, these loads are deposited and not only supply natural ecosystems, for example riparian forests, with nutrients, but also supply agroecosystems. For example, the sediments deposited during the flooding of the Nile had existential importance for the agriculture of Egypt for thousands of years. Removal of natural vegetation by humans increases soil erosion, which also increases the amount of material transported by rivers. The clearing of forests in Central Europe, which began with the spread of agriculture 7,000 years ago, led to filling of stream and river flood plains with fertile soil. In the tropics, because of greater precipitation, the clearing of forests often results in devastating landslides that can destroy entire villages in the valleys. In addition, the rivers transport the removed soil to the ocean, where coral reefs are buried by the sediment and subsequently die. As a result, populations of fish species directly or indirectly dependent on the reefs also decline, which in turn threatens the food supply and livelihoods of many coastal residents.

Material transport through **wind** is also of great importance for many ecosystems. During the Ice Ages, loess, i.e. silt produced by the movements of glaciers on rocks, was formed. On poorly vegetated areas, this material was subject to wind erosion and was, in some cases, deposited in great layers in other locations. Loess forms fertile soils that are among the best agricultural lands in many areas of the world (e.g. China, North America, Central Europe). Today, wind-related transport processes are still important. Over a distance of more than 5,000 km, millions of tons of sand and dust are transported from the Sahara to the Amazon region every year. This is a significant source of nutrients for the rain forest there.

Input of nitrogen from the atmosphere is an (additional) source of nutrients for several ecosystems (Sect. 3.7.4.2).

Ecosystems are not closed entities, but instead are connected with each other through the interactions of species, as well as through the flow of energy and materials.

3.5.3 Flows of Energy and Material in Agroecosystems

With regard to energy and material flows, intensively managed agroecosystems, in particular, have several characteristics distinct from those of natural ecosystems:

- Large proportions of the net primary productivity, i.e. the biomass of the crops, are removed from the system during harvest, which also results in a decline in the nutrient content of the soil.
- To compensate for these losses, fertilizers must be used (Sect. 2.3.3). Mineral fertilizers are imported into the agroecosystem from outside and must be produced and transported using energy, which in turn uses external resources, primarily fossil fuels.
- For the production of crops, further energy is required, specifically for soil cultivation, sowing, harvest, and possibly irrigation. This energy comes from manual labour, the use of animals or the application of machinery and is based on food, feed, or fuel, respectively. Usually, chemicals are also applied to control pests, weeds, and phytopathogens. These substances must also be produced, transported, and distributed. Their residues reach the food webs and ecosystems.
- Only a relatively small portion of the nutrients imported into an agroecosystem as fertilizers is taken up by the crop plants. For example, only approximately one third of the nitrogen applied to the soil in German agriculture is extracted via the plant and animal products. The rest is leached out or escapes as a gas into the atmosphere (Sect. 3.7.4.2). Sixty percent of the nitrogen input into the North and Baltic Seas originates from agriculture.
- Through global trade, agricultural products (e.g. cereals and soybean for animal production) reach other regions where they become a component of the material and energy flows of those ecosystems (e.g. in the form of animal excrement).

Intensively cultivated agroecosystems in particular are characterized by high material and energy flows and to only a limited extent by internal cycles.

3.6 Ecosystem Services

The present and future welfare of people, societies, and economies depend on the various goods and resources provided by nature. Beside the many kinds of plants and animals from agricultural and natural systems that sustain and benefit human life, this also includes a variety of services, often considered as granted and freely available. They are so-called public goods, which cannot be owned and have no markets and prices. Such services are based on natural ecosystem processes and functions, which result in the provision, regeneration, and long-term stability of