Chapter 7
Forest landscape change and biodiversity conservation

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Abstract Forest landscapes are changing at unprecedented rates in many regions of the world. This may have profound consequences for the diversity and resilience of forest ecosystems and may impose considerable challenges for their management. In this chapter, we review the different types of change that can occur in a forest landscape, including modifications in forest habitat amount, quality, fragmentation, connectivity, and heterogeneity. We describe the conceptual differences and potential interactions among these changes and provide a summary of the possible responses of forest species depending on their degree of habitat specialization, dispersal abilities, and other factors. We review the main current drivers of change in different regions of the world and how they are affecting (often synergistically) forest biodiversity: deforestation, climate change, forest fires, abandonment of rural land, land-use intensification, spread of invasive species, forest management, and the increasing amount of plantation forest. We conclude by providing a summary of recommendations and strategies for mitigating and minimizing the undesirable effects of landscape change on forest biodiversity.

7.1   Introduction

Despite increasing conservation efforts (Rands et al. 2010), global biodiversity, which comprises the diversity of life in all its forms and levels of organization (Hunter and Schmiegelow 2011), has declined in recent decades (Butchart et al. 2010)

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and is projected to continue diminishing throughout the twenty first century (Pereira et al. 2010, Sala et al. 2000). Tropical forests are being converted to other land uses, mainly to agriculture, at high rates, and the remaining forest fragments are increasingly small and isolated. The consequent reduction in populations of many forest species may compromise their persistence in the future, in part because their growing isolation may lead to adverse metapopulation dynamics, and may even generate genetic bottlenecks. The decline in functional connectivity among forest populations is being exacerbated by a worldwide intensification of agricultural practices that makes the matrix in which forest fragments are embedded less permeable. Moreover, as the length of the boundaries between forests and adjacent non-forest lands increases in the landscape, the effective area of suitable habitat for many forest species will be reduced because they are not adapted to conditions found at the forest's edges. Fragmentation of tropical forests, combined with droughts induced by climate change, is also favoring an increased fire occurrence, possibly beyond the limits to which these ecosystems may be resilient. The resilience of fire-prone forest ecosystems (e.g., many Mediterranean and some North American temperate forests) may also be compromised by current and foreseen alterations in their historical fire regime. Another key global process that influences forest biodiversity is climate change. Climate change is expected to trigger shifts in species distribution poleward and upward in altitude, driving a worldwide rearrangement of forest species. Species responses to climate change will be idiosyncratic, especially given novel biotic interactions that may appear or be substantially altered as a result of climate warming. Furthermore, the capacity of forest species to adapt to changing climatic conditions may be curtailed by the aforementioned loss in connectivity. Forest species are already confronted by all these processes and by others, such as a reduced quality of forest habitats around the world, changes in landscape heterogeneity, or invasion by exotic species, leading to a complex set of interactions and synergies among these processes.

In this chapter, we describe how agents of global change influence forest biodiversity from a landscape-scale perspective, with a particular focus on conceptual mechanisms. By understanding these mechanisms, we may be able to anticipate and better avoid potential negative effects on each forest species. The responses to these processes are expected to differ among species, with their vulnerability depending on diverse aspects such as body size, geographical range, dispersal ability, reproductive rate, and niche specialization (Brook et al. 2008). This means that any particular landscape change that may jeopardize some species may also favor other species. In general, forest specialists are expected to be more negatively affected than generalist species by ongoing landscape changes, with a consequent potential homogenization of biota across regions. Overall, the potential future scenarios of global biodiversity loss addressed throughout this chapter provide an argument for the need to adopt political, economic, and social measures to reduce these pressures. For that purpose, we present some general management guidelines in the last section of the chapter.

7.2   Types of change in the forest landscape and their influences on forest biodiversity

7.2.1   Habitat loss and fragmentation: related but conceptually different processes

Habitat can be defined as the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a particular species (Hall et al. 1997). Habitat is therefore species-specific. Habitat loss is the reduction of the amount of habitat for a particular species in a landscape, and therefore negatively affects the abundance of that species, sometimes even causing its disappearance. The habitat for a particular forest-dwelling species may correspond to a specific forest composition and structure (e.g., one or more successional stages or even non-forest vegetation in part of its life cycle). Therefore, habitat loss for a species should not necessarily be associated with the loss of forest cover in general. Nonetheless, forest cover is a critical element for the persistence of most forest species, and analyzing changes in its abundance and configuration is a helpful approach, as we will summarize in Sect. 7.2.5.

A related but conceptually different process is habitat fragmentation, which can be defined as the process through which large and continuous habitat patches are broken apart into multiple smaller pieces that are physically separated from each other (Haila 1999). The potentially negative effects of habitat fragmentation for biodiversity conservation have been widely described (e.g., Fahrig 2003), and are generally grouped in three categories: reduced patch size, patch isolation, and edge effects.

Habitat patches in the landscape become smaller with increasing fragmentation. From the perspective of an individual species, a reduction in the effective population size in smaller habitat fragments increases the probability that a species will go locally extinct, which is known as the "small-population" paradigm (Caughley 1994). Many theoretical and empirical studies have focused on evaluating the minimum number of individuals required for the persistence of a species within a specified timeframe, the so-called minimum viable population size (Shaffer 1981, Traill et al. 2007). Fragmentation may also increase isolation among previously continuous habitat patches as they become separated by unsuitable areas and as the distance between them increases. The small-population paradigm has traditionally assumed that populations are isolated. Yet both island biogeography theory and metapopulation theory (Hanski 1999) highlight the possibility that a small population can persist through immigration of individuals from other populations in the surrounding landscape. This has led to a more recent approach based on considering all of the populations in a landscape through the use of the "minimum viable *metapopulation* size" concept (Bulman et al. 2007). In short, the negative impact of habitat loss on biodiversity may be attenuated to some degree when functional connectivity is maintained. Theoretical studies predict that the extinction threshold will be reached

later in the gradient of shrinking habitat amount in less isolated (more connected) sets of patches (Fahrig 2002), something we will discuss in Sects. 7.2.2 and 7.2.5. We will explore the impacts of habitat isolation on forest biodiversity in more detail in Sect. 7.2.2, on landscape connectivity.

Species richness declines with diminishing patch area (size), and this is one of the most consistent patterns in ecology (Begon et al. 2006). Much of the research on the effects of reduced patch size and patch isolation on community species richness has been framed within the theory of island biogeography (MacArthur and Wilson 1967), in which patch area and isolation are drivers of the extinction and immigration dynamics of populations. Apart from the island biogeography framework, many other possible underlying causes for decreases in species richness have been hypothesized, such as parallel decreases in environmental diversity, available energy, the target area for colonizers, or the number of sampled individuals (see Gardner and Engelhardt (2008) and the references therein). This consistent species richness–area pattern has allowed the common use of species–area curves to predict future species extinctions that will follow the loss of forest cover (e.g., Pimm and Raven 2000); we will discuss this in more detail in Sect. 7.3.1, on deforestation.

The "edge" of a habitat patch is the portion near the patch's perimeter. Many forest species avoid forest edges or have lower population densities near them. These patterns, called "edge effects", are driven by a variety of factors such as increased predation risk, modified microclimates, more intense human disturbances, and higher competition with generalist species at the patch edges than in the core areas (Gonzalez et al. 2010, Laurance et al. 2006). The distance from the border reached by edge effects is species dependent, but as forest fragmentation proceeds, all edge-sensitive species will begin to suffer from larger reductions in the area of their effective core habitat rather than in the total amount of forest in the landscape. Examples of edge-sensitive species include many lichens (e.g., Rocío et al. 2007) and bryophytes (e.g., Löbel et al. 2012), but specific cases are common for all taxonomic groups (e.g., vascular plants, birds, mammals).

Forest area loss and fragmentation are recognized as the main factors behind decreases in forest biodiversity, but disentangling their relative importance is not easy. Both changes usually occur simultaneously through the processes of deforestation and habitat degradation (the change from A, through B and C, to D in Fig. 7.1). This has frequently led to an overestimation of the actual effects of forest fragmentation on species persistence. Imagine, for example, that ten forest species were found in landscape A in Figure 7.1, and that the change process that goes from A to D in that figure (with B and C as intermediate stages) would have reduced the number of species to only two. This has been interpreted in many cases as the basis to conclude that forest fragmentation has caused the loss of 80 % of the original species richness (i.e., a loss of eight species). However, in the process of changing from A to D, fragmentation has not been the only important change; the amount of habitat has also decreased greatly for many forest-dwelling species. It would be interesting to know how many forest species would have been lost if a different change process had occurred (such as from A, through E, to F in Fig. 7.1); that is, if the same amount of forest area had been lost but with no fragmentation occurring (stage F, in
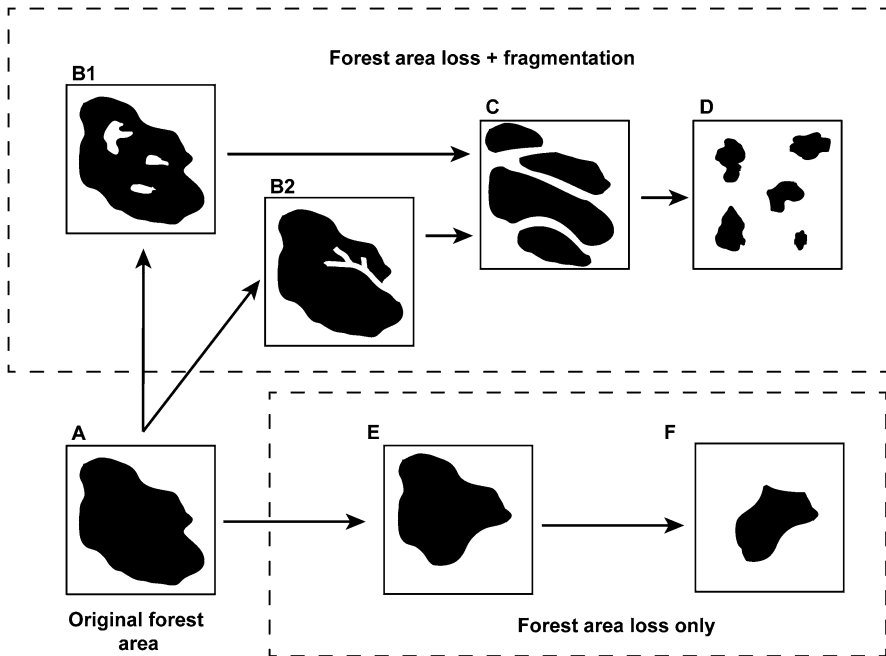
Figure 7.1 Changes in the amount and spatial arrangement of forest cover that can occur as a result of forest area loss and fragmentation processes. The upper box (changes from A, through B and C, to D) illustrates the typical progression of a process with combined loss of forest area and fragmentation, whereas the lower box (changes from A, through E, to F) corresponds to the case in which forest area is lost without causing any breaking apart of the remnant forest. B1 and B2 are two alternative possibilities for the typical spatial changes that would occur before separated patches are produced during the change from A to D. The final stages in both cases (D for the upper box and F for the lower one) have the same amount of forest area, but with a different spatial arrangement

which the total forest area is the same as the total in stage D). If, for example, four of the original ten forest species were found in stage F, this would mean that habitat loss alone has been responsible for the loss of six species, whereas the impacts of fragmentation per se have only caused the loss of two additional species (i.e., the difference in species richness between stages F and D). For habitat fragmentation to happen, some habitat loss needs to occur, even if this is only a small amount; for example, if the incisions in landscape B2 in Figure 7.1 continue to progress, they would break the forest into several separated patches with a relatively minor reduction in total forest area. However, the opposite is not true, since habitat loss can happen without any fragmentation or breaking apart of habitats (as in the change from A, through E, to F in Fig. 7.1). A meta-analysis by Fahrig (2003) showed that habitat loss has more prominent and consistent detrimental effects on biodiversity than habitat fragmentation. Forest fragmentation can indeed have important nega- tive effects on biodiversity (e.g., Laurance et al. 2006) but, in general, fragmentation

will be responsible for only a part of the total impacts on species and populations. For forest landscape management planning, it will be useful to disentangle the relative importance of these two processes for a particular species; that is, it is important to learn whether the focus should be placed more on the spatial configuration of the habitat patches or more on the total amount of habitat in the landscape.

7.2.2   *Landscape connectivity*

Based on Taylor et al. (1993), landscape connectivity can be defined as the degree to which the landscape facilitates movement among the existing habitat resources for a given species. Managing landscape connectivity is a key part of forest biodiversity conservation, as it is considered to be one of the best strategies for counteracting the adverse effects of fragmentation and facilitating shifts in species ranges in response to climate change (Araújo and Rahbek 2006, Opdam and Wascher 2004, Taylor et al. 1993).

Fragmentation and connectivity loss are related, but different, concepts. Fragmentation is a structural property in which patches of habitat are subdivided and physically separated from each other, and can be measured and assessed without considering the dispersal abilities of any particular organism. In contrast, landscape connectivity is a functional, species-specific property that depends on the dispersal abilities and behavioral traits of a given species (Theobald 2006, Tischendorf and Fahrig 2000). A given landscape might be perceived as strongly connected for an organism able to traverse large distances (e.g., a bird species), whereas it might be weakly connected for another species dwelling in the same landscape that only disperses over short distances, that lacks the ability to move through the land cover types in the landscape matrix that separates its habitat areas, or a combination of both (e.g., an amphibian). Fragmentation can occur without an impact on the connectivity among remnant patches; for example, for a bird species with a high movement ability, all the patches in landscape D in Figure 7.1 may still function as a single fully connected unit. On the other hand, connectivity losses can occur even with no additional habitat fragmentation. This will occur when a given landscape change does not directly affect the area of habitat, but impedes the dispersal of a species between habitats due to increased resistance to dispersal in the landscape matrix (e.g., as a result of road construction, urban development, or intensification of agriculture).

The concept of connectivity has often been associated with the presence of corridors, which are conceived as narrow, elongated strips of vegetation that physically connect larger blocks. However, the options to promote landscape connectivity go well beyond the maintenance or establishment of corridors. Ecological fluxes among habitat areas can also occur in a more diffuse but equally effective manner through wide stretches of a permeable non-habitat landscape matrix or by means of successive short-range movements facilitated by a series of stepping-stone habitat patches, such as small woodlots, or even single trees scattered throughout the landscape (Adriaensen et al. 2003, Lindenmayer et al. 2012, Manning et al. 2009, Rey Benayas et al. 2008, Uezu et al. 2008, With et al. 1997).
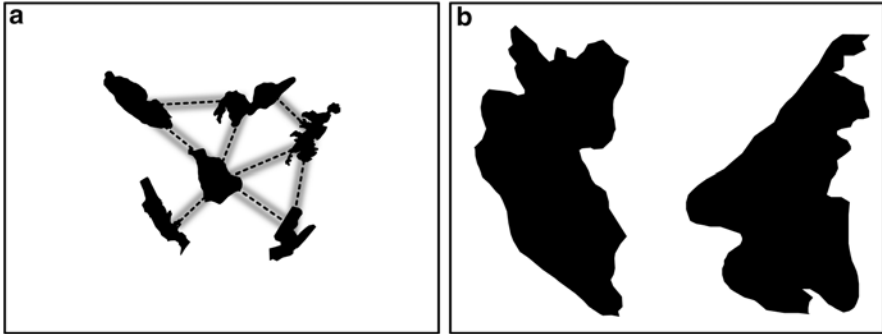
Figure 7.2 Two simple hypothetical landscapes (**a**, **b**) with different sets of habitat patches (shown in *black*) and links (direct connections) between them (shown as *dashed lines* with *grey* shadows) for a given species to illustrate the concept of habitat availability (reachability) at the landscape scale (see the main text for details). Links represent functional connections between the patches; that is, they represent the ability of a given species to move between patches, and may correspond to the existence of a corridor, of a permeable landscape matrix that makes movement of a species possible, or of a series of stepping stones that facilitate dispersal between source and destination habitat patches. Adapted from Saura (2008)

One of the classical definitions of landscape connectivity was provided by Taylor et al. (1993): "the degree to which the landscape facilitates or impedes movement among resource patches". This definition suggests that landscape connectivity can be successfully addressed and managed by considering only the number and quality of the connections among habitat patches. However, an approach that focuses only on the connections between habitat patches (interpatch connectivity) can mislead conservation managers when it deals with landscape changes that affect both the size and the spatial configuration of the patches. Consider the two landscapes in Figure 7.2, which shows the distribution of habitat patches and the links (functional connections) among them for a given focal species. Which landscape is more connected? It may seem obvious that connectivity is higher in **a** than in **b**, because in **a** there are eight links between patches, whereas in landscape **b** there are none. However, from a management perspective it makes no sense to consider **a** as more connected than **b** because no matter how well connected the patches are in landscape **a**, collectively they comprise less available (reachable) habitat than the area in only one of the patches in landscape **b** (Pascual-Hortal and Saura 2006, Saura 2008). In other words, a big isolated patch in **b** comprises a larger area of connected habitat within itself than all the area that can be reached through all the links in landscape **a**. As noted by Tischendorf and Fahrig (2000), some connectivity metrics suffer from the problem of indicating higher connectivity in more fragmented landscapes and zero connectivity in any landscape containing just one habitat patch, even if that habitat patch covers the whole landscape.

To provide an appropriate measure of landscape connectivity in changing landscapes: (1) the amount of connected habitat within habitat patches has to be considered (bigger patches have more intrapatch connectivity), even when the patches are completely isolated from all other patches, and (2) intrapatch connectivity must

be considered along with the area made available by the connections with other habitat patches (interpatch connectivity). This is the concept of habitat *availability* (reachability) at the landscape scale (Pascual-Hortal and Saura 2006, Saura 2008, Saura and Pascual-Hortal 2007, Saura and Rubio 2010). Fundamentally, it means that connectivity should be considered as a landscape property that allows a particular species to reach a larger amount of habitat resources, no matter if these resources are provided by a single big patch (intrapatch connectivity), by the connections between different patches (interpatch connectivity) or, more frequently, by a combination of both. If connectivity is relevant for management, this is because it increases the amount of habitat that can be reached by a particular species in the landscape, not because it increases the number of connections between increasingly smaller and poorer habitat patches (as in landscape **a** in Fig. 7.2).

New metrics have been proposed that are derived from this way of conceiving and measuring connectivity (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007), and they have been implemented in the Conefor software (http://www.conefor.org) and widely applied to support landscape connectivity conservation management in different countries. Among these, the equivalent connectivity area (*ECA*) is an intuitive and useful metric that is defined as the size that a single habitat patch should have in order to provide the same amount of reachable (available) habitat (i.e., connectivity) as the mosaic of habitat patches in a given landscape (Saura et al. 2011a, b). *ECA* will be equal to the total area of habitat in the landscape (*A*) for a particular species when either all of the habitat is concentrated in a single continuous habitat patch or when the habitat is dissected into different patches but the probability of movement between any two patches is equal to 1 for that species. With this approach, it is possible to directly compare the relative change in *ECA*, d*ECA* = (final − initial)/initial, with the relative change in the total amount (area) of habitat in the landscape, d*A* = (final − initial)/initial, after a given landscape change (Fig. 7.3). This allows an assessment of the degree to which a given change in the total amount of habitat would be beneficial or detrimental for ecological connectivity. For example, a net decrease in the total amount of habitat (d*A* < 0) may translate into a higher, lower, or equal loss of connectivity as measured by d*ECA*, as illustrated in Figure 7.3 (respectively) by the cases in which d*ECA* < d*A* < 0 (higher loss in the amount of reachable habitat than in the total habitat area), d*A* < d*ECA* < 0 (higher loss in the total habitat area than in the amount of reachable habitat), and d*ECA* = d*A* < 0 (both magnitudes decrease at the same rate, corresponding to a purely proportional effect of habitat loss).

Figure 7.3 (continued) analyzed period ("stable forest"), be lost due to conversion to other cover types ("forest loss," in which initially forested areas are no longer forested at the end of the period), or expand as a result of afforestation ("forest gain," in which areas that were not forested in the past are covered by forests at the end of the period). The six types of change correspond to the evolution of real Spanish landscapes, as they were selected from some of the samples in the SISPARES monitoring system (http://www.sispares.com). The figure was adapted from Saura et al. (2011b). See Saura et al. (2011a, b) for further details
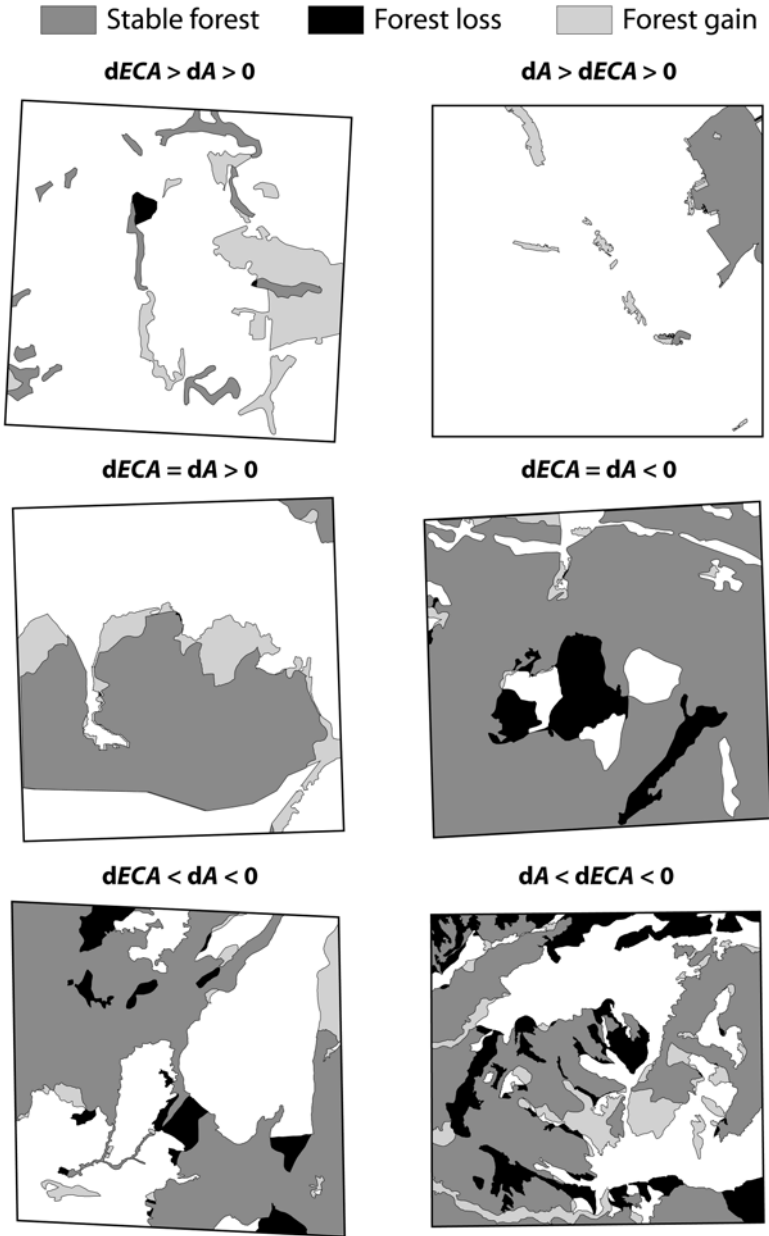
Figure 7.3 Six different landscapes (each covering 4×4 km) that illustrate the different ways in which the change in the total amount of habitat (d*A*) in a given time period can translate into a higher or lower change in the connectivity of the habitat in the landscape (d*ECA*), which is measured here by the equivalent connected area (*ECA*) for a species with a median dispersal distance of 200 m (relative to the landscape extent of 4×4 km). The examples in this figure assume that forest is the focal habitat. The areas occupied by forests may either remain stable during the

7.2.3 Habitat quality in the forest landscape

Even if habitat patches in the landscape are not completely eliminated or reduced in size, significant population declines or even species losses can occur due to the reduction in their quality as a result of natural disturbances or, more frequently, human interventions such as logging, grazing of livestock, or hunting. For example, for many forest specialist species, the abundance of elements characteristic of old-growth forests is an indicator of a forest's quality as habitat (e.g., Grove 2002, Lindenmayer et al. 2012). These elements include thick stems, dead wood in a range of diameter classes, an uneven-aged structure, and vertical (multilayer) or horizontal (spatial) heterogeneity. However, because habitat quality is, by definition, species-specific, the modification of some habitat characteristics may impair some species while favoring others. For example, microclimatic changes after harvesting may be detrimental to shade-tolerant plant species, whereas the increased availability of ground vegetation associated with early successional stages would benefit other organisms such as large herbivores.

For many ecologists and environmentalists, the quality of a forest ecosystem is largely determined by its degree of naturalness. This perspective requires an ecological baseline; that is, it requires historical information about the conditions under which the ecosystem developed. However, human influences on ecosystems may be difficult to disentangle from natural ones, especially in regions such as Europe, where centuries of human land use have left a deep footprint (see Hermy and Verheyen 2007 for a review; Rozas et al. 2009). For example, soil nutrient levels and the species composition in afforested patches can be influenced by former agricultural land use (Hermy and Verheyen 2007), and these changes have been observed to last as long as 2000 years (Dupouey et al. 2002). Even the use of pre-European conditions in North America as archetypes of pristine ecosystems has been criticized, since this probably underestimates the role of aboriginal peoples in shaping the landscape (Alagona et al. 2012). This situation is compounded by the dynamic and changeable nature of ecosystems even in the absence of human interference (Alagona et al. 2012). Furthermore, future uncertainty due to rapidly changing climatic and environmental conditions further challenges the search for an ecological reference to define the generic quality of a particular forest ecosystem.

7.2.4 Forest landscape heterogeneity

Different sets of species are associated with particular forest types and land covers, or combinations of types and covers. Therefore, it will generally be the case that heterogeneous forest landscapes, which comprise multiple forest and non-forest types, are able to harbor a relatively large number of species. Indeed, the importance of spatial heterogeneity for diversity has been long recognized as

one of the central concepts in landscape ecology. The increase in species richness with landscape heterogeneity might be due to (1) a higher gamma diversity resulting from nonoverlapping sets of specialist species being present in different land cover types (beta diversity); (2) the fact that some species use resources from different cover types (generalist or heterogeneity-dependent species), such as raptors that nest in forests but forage in adjacent pastures; or (3) a combination of the two.

However, increasing heterogeneity is not necessarily beneficial for biodiversity conservation in many situations. Landscape heterogeneity cannot be increased without reducing the extent of some land cover types within the landscape, and this may or may not be a desirable outcome. The potential benefits of heterogeneity depend on the conservation value of the affected forest or cover types and their associated species. In fact, some regions of the world that are undergoing biodiversity loss are at the same time experiencing considerable increases in landscape heterogeneity, because they are in the initial stages of forest cover loss and fragmentation. These regions are shifting from large areas covered by primary, species-rich forests (which may be regarded as relatively homogeneous landscapes) to landscapes in which heterogeneity is increased by a variety of new cover types such as pastures, cropland, and urban areas. The assumed benefits of landscape heterogeneity may vanish when the conservation status of each species, and not just the total number of species, is taken into account. There is the risk of favoring generalist, cosmopolitan species by promoting landscape heterogeneity as a general management principle. Any landscape-scale change has losers and winners, and it is the identity and particular status of each of the affected species that should determine whether a particular type of change should be promoted in a given forest conservation management plan.

7.2.5   *Responses of forest species abundance and diversity to landscape change: a summary of scenarios*

In this section, we integrate the different types of landscape change described in previous sections to provide a conceptual summary and a comparative assessment of their potential impacts on the abundance of a particular forest species. We mainly borrow from Andrén et al. (1997) and Brotons et al. (2005), with several adaptations and additions for the purposes of this chapter. We consider different scenarios regarding the potential responses of a species to landscape change, depending on the species' habitat requirements, on its dispersal abilities, and on the dominant type of landscape change. Since the response of an entire forest species community to landscape change will be the aggregated result of the response of each individual species (and of the interactions among them), this conceptual synthesis will also help to predict how community richness might be affected by habitat loss, fragmentation, reduced landscape connectivity, decreases in habitat quality, or variations in landscape heterogeneity.

7.2.5.1   Potential responses of a forest specialist species
to landscape change

First, we consider the case of a strict forest specialist species, which has a particular forest type (hereafter referred to as "F" for simplicity) as its only habitat in the landscape. It therefore follows that the maximum population levels for this species will be found when the entire landscape is occupied by F. In this case, there are three possible species responses to habitat loss:

– *A purely proportional effect of habitat loss (scenario S1 in Fig. 7.4).* Species abundance responds linearly (and in exact proportion) to the reduction of the cover of forest type F in the landscape because the population size is limited only by the total amount of habitat. There are no other additional impacts that compound habitat loss, even for low levels of habitat cover, such as those that might arise from habitat fragmentation. This might be the case for species that are largely insensitive to edge effects and that are able to satisfy their vital needs even in disturbed landscapes that retain a small amount of habitat area. These are typically species with small home ranges and small body masses, such as rodents.
– *A critical threshold in the habitat amount (scenario S2 in Fig. 7.4).* This is characterized as an abrupt decline in population size when the amount of habitat in the landscape drops below a certain threshold, as has been reported in simulation studies (With and King 1999) and, to a lesser extent, in empirical landscape studies (see Swift and Hannon 2010 for a review) for species such as the northern spotted owl (*Strix occidentalis caurina*) or the white-backed woodpecker (*Dendrocopos leucotos*). The proportional response in scenario S1 might hold until the amount of forest type F that remains in the landscape falls below a certain level, after which the species might go extinct or suffer from an abrupt decline. (See Sect. 7.2.1 for additional discussion.)

If the species is highly mobile and readily ventures through the non-habitat matrix, it might perceive all of the forest type F in the landscape as a single functionally connected unit. In this case, the amount of available (reachable) habitat in the landscape will be the same whether or not the landscape change corresponds to a pure habitat loss (the change from A to F in Fig. 7.1) or to the case in which fragmentation occurs with the remnant patches getting separated from each other (the change from A to D in Fig. 7.1). The critical threshold would therefore occur for much the same amount of habitat in both change types, assuming that no other compounding effects (such as an increased edge influence in the fragmentation case) affect the focal species. However, if the species is unable to move through cover types that differ from F, the available habitat area will correspond only to the size of the occupied habitat patch. In this case, an abrupt response could occur with just a small additional loss of forest type F if that loss fragments the habitat into several patches that are all smaller than the minimum viable size. In this case (low connectivity), an abrupt decline in population will appear earlier in the fragmentation process (during the change from A to D in Fig. 7.1). Therefore, the effects of habitat fragmentation and reduced connectivity may intensify the effect of these critical thresholds.
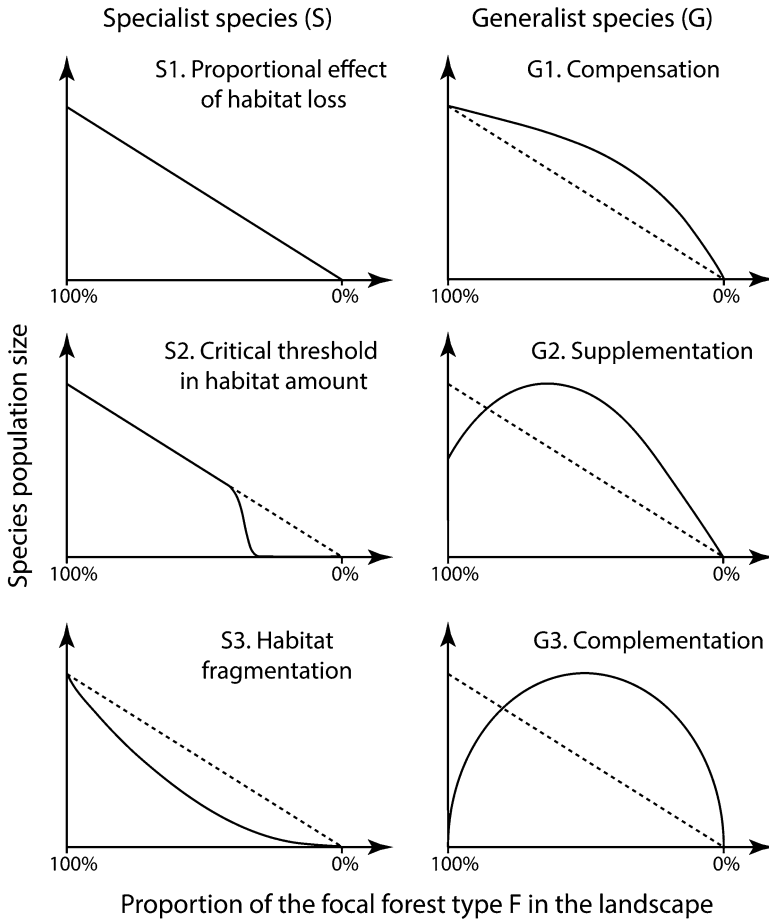
Figure 7.4 Hypothetical scenarios for the response of the population of a forest species to the loss of varying amounts of a given focal forest type F. The species is assumed to have F either as its only habitat (specialist species; S scenarios) or as a part of the habitat resources it requires to fulfill its vital needs (generalist species; G scenarios). The *y*-axis shows an arbitrary scale ranging from the maximum attainable population size to the absence (extinction) of the species in the landscape. The response curve for scenario S1 is added as a reference (*dashed line*) in all the other scenarios. See Sect. 7.2.5 of the text for a description and discussion of the six scenarios and their relationships to different species traits and types of landscape change. Adapted from Andrén et al. (1997) and Brotons et al. (2005)

However, such thresholds may also appear in the absence of fragmentation (during the change from A to F in Fig. 7.1; Swift and Hannon 2010).

– *Habitat loss has an amplified impact on the population size due to fragmentation and reduced connectivity (scenario S3 in Fig. 7.4).* A given percentage loss of forest type F translates into a proportionately larger reduction in species abundance, so the population size falls below the linear response depicted in scenario S1 (Fig. 7.4).

This is typically the case for fragmentation-sensitive species. Even in the early stages of the fragmentation process, when only a small amount of habitat has been lost and the forest has not yet broken apart (e.g., the perforations in B1 or the incisions in B2 in Fig. 7.1), the core area (the area away from the edges of the patch) will be reduced much more than the total patch area, leading to a comparatively large population reduction for edge-sensitive species. (For more discussion of edge effects, see Sect. 7.2.1.) In addition, some of the fragment sizes may fall below that required to support the minimum viable population size for some species. If a species has poor dispersal ability or if the habitat is embedded in a non-permeable matrix, the lack of functional connectivity will produce a larger decrease in the usable and reachable habitat area than the actual decrease in the total habitat area (e.g., see the case $dECA < dA < 0$ in Fig. 7.3).

Typically, some fragments below the minimum viable size will be produced all along the gradient of habitat loss and fragmentation, and therefore such amplification of the impacts of habitat loss is likely to translate into a continuously decreasing response curve that falls below the linear change in scenario S1. However, the proportion of the habitat that falls below the minimum patch size may typically increase for lower levels of total habitat amount, and the increase in the distance between patches will generally be larger in landscapes where habitat is already sparse (Andrén 1994), making dispersal limitations translate more easily into effectively isolated populations in individual patches. This could lead, in the extreme, to the sharp critical threshold described in scenario S2, although it will probably lead to a milder response that lies somewhere between scenarios S2 and S3 (Fig. 7.4). Amplified impacts of habitat loss might also occur due to a reduced permeability in the landscape matrix (e.g., from agricultural intensification or road construction). Extinction debts (time lags in species responses) may also make the response curves vary from S1 to S2 or S3 over time (Tilman et al. 1994), even when no additional changes in the habitat or landscape occur.

7.2.5.2 Potential responses of forest generalist species to landscape change

In the previous three scenarios, we considered the case of a hypothetical forest specialist species that had forest type F as its only habitat. Now we relax that assumption to incorporate the effects of landscape heterogeneity on species responses. We now consider a generalist species that requires some amount of the focal forest type F to fulfill its vital needs, but that can also use resources in other forest or cover types. In this case, complete loss of the focal forest type F would lead to disappearance of the species, but it is not clear how its population size would react to smaller changes in the amount of F. This will depend largely on the species' traits and on the characteristics of the other forests or land covers to which F is converted. We can, however, conceptually differentiate three distinctive responses and

link these to different ways in which particular changes in landscape heterogeneity could affect forest biodiversity:

– *Landscape compensation* (scenario G1 in Fig. 7.4). In this scenario, type F is converted to other forest or cover types that have some resources suitable for the species, although in smaller quantities or with lower quality than in F. Thus, they can partially compensate for the loss of focal forest F, and the population size would decrease, but at a lower rate than the amount of F that is lost; that is, the response curve would remain above the linear (proportional) response of scenario S1. Examples of compensation have been found, for example, for some bird species that had natural steppes as their primary habitat but that could potentially use extensive pastoral habitat (Brotons et al. 2005). This scenario would also apply when a decrease in the *quality* of F, rather than complete disappearance of this type, occurs. (See Sect. 7.2.3 for more discussion of the effects of habitat quality.) Depending on the amount of resources in the areas where F has been lost or degraded, higher or lower compensation levels will occur, with the response curve for scenario G1 in Figure 7.4 falling either farther from or closer to that for scenario S1.
– *Landscape supplementation* (scenario G2 in Fig. 7.4). This will occur when the other forest or cover types that substitute for F present some additional valuable resources for the species that are not available in F (Dunning et al. 1992). The species will therefore increase its resource intake in landscapes where both forest or cover types coexist, benefiting from that heterogeneity more than in the case in which only F is present in the landscape. In the study by Brotons et al. (2005), some steppe bird species were benefited by the presence of nearby pastures, probably due to the increased abundance of insects. However, at some point, loss of F is so large that the disadvantages outweigh the benefits, and the population of the species begins to decline again.
– *Landscape complementation* (scenario G3 in Fig. 7.4). Some species may be unable to find all the resources they require to complete their life cycle (e.g., foraging areas, shelter areas, winter roost sites, breeding patches) in a single cover type. Such species would depend on the combined presence of different forest and cover types, each providing different, complementary, and non-substitutable resources (Dulaurent et al. 2011, Dunning et al. 1992). Therefore, a landscape dominated only by F may not provide all the required habitat for some forest species, and the conversion of F into other forest or cover types, or their coexistence, would represent the optimal landscape setting for these mosaic- or heterogeneity-dependent species. As an example, many large herbivores or game birds such as *Perdix* spp. need to complement food resources from open areas with the proximity of forests that provide refuge (Choquenot and Ruscoe 2003). However, as in the supplementation scenario, there is a point at which the loss of F produces disadvantages that outweigh the benefits from a more diverse landscape, resulting in a decline in species population size.

Whether any of these effects occur (compensation, supplementation, complementation), and the intensity of the effects, will depend not only on the amounts of

the different forest and cover types in the landscape but also on the ability of a species to move among patches. For species with movement limitations in a given landscape, the complementary or supplementary resources that may exist in other forest or cover types that are different from F may only be reachable when the different patch types are distributed in close proximity to each other; that is, there must be a fine-scale mixture between the different covers. For the same reason, reductions in the permeability of the landscape matrix, even when they do not directly affect the area or quality of any of the cover types that are used as habitat by the species, may bring any of the generalist response curves closer to the curve in scenario S1 (Fig. 7.4) or even below that curve if species are benefited by (G2) or require (G3) those other difficult-to-reach resources.

The combinations of different types of change occurring in the landscape and their interaction with the particular traits of a species will determine the final response of each forest species, or of the total forest species richness, in the landscape. The resulting response might be close to one of the six idealized response scenarios in Figure 7.4, but it is more probable that it would fall somewhere between these scenarios due to the aggregated result of the different processes described earlier in this Section.

7.3 Major contemporary processes driving forest landscape changes and their impacts on forest biodiversity

7.3.1 Deforestation

Forest loss (deforestation) is a key driver of current global biodiversity loss. Current rates of forest conversion, mainly to agricultural uses, have raised the alarm about the future of biodiversity, particularly in the tropics (Bradshaw et al. 2009a, Laurance 2007), with the expected effects even larger than those predicted as a result of future climate change (Sala et al. 2000). Although tropical forests represent only 7 % of the Earth's land surface (Bradshaw et al. 2009a), an important portion of global biodiversity depends on the persistence of tropical forest habitats (Dirzo and Raven 2003); therefore, deforestation in these regions is an important threat to global biodiversity. Many studies have estimated high rates of species extinctions in tropical forests based on rates of forest loss combined with species–area curves; for example, see some of the figures and references in Bradshaw et al. (2009a), Brook et al. (2008), and Laurance (2007). However, the wide discrepancy between predicted rates at a global scale and those that have actually been recorded (much lower) has fostered a debate about how to explain this disagreement (He and Hubbell 2011, Ladle 2009). Although there seems to be a better agreement at local and regional scales (Fattorini and Borges 2012), the species–area relationship, even when based on endemic species from the area of forest being destroyed, only

estimates instantaneous extinction. However, many species that survive under suboptimal conditions in small forest fragments may already be committed to extinction when the conditions for their reproduction are no longer met—the so-called extinction debt (Tilman et al. 1994). A more realistic framework that includes potential extinction has recently been introduced to account for these issues (Tanentzap et al. 2012). Finally, it is important to note that, even if forest is restored, ongoing anthropogenic disturbances in deforested areas are expected to have a legacy effect on their habitat quality (see Sect. 7.2.3), for example, through an accumulation of persistent pesticides.

Deforestation often results in fragmentation of the remaining forest. (For a more detailed discussion of fragmentation, see Sect. 7.2.1.) The species composition and structure of remnant forests have been reported to differ from those of previously continuous forests in many studies (e.g., Benedick et al. 2006, Filgueiras et al. 2011, Watson et al. 2004). Furthermore, some authors warn about the convergence of species composition in small forest fragments to the composition of communities adapted to early successional vegetation, inducing the replacement of forest interior (edge-sensitive) species by generalist, disturbance-tolerant species across the landscape (e.g., Laurance et al. 2006, Lôbo et al. 2011). Although this speaks to the irreplaceability of large, continuous forests, some authors also highlight the conservation value of networks of small fragments, given their potentially substantial contribution to landscape-level biodiversity through increased heterogeneity (e.g., Bell and Donnelly 2006, Struebig et al. 2008) and functional connectivity (but see Sects. 7.2.2 and 7.2.4).

7.3.2 Abandonment of rural land

In some regions of the world (and particularly in some developed countries), the abandonment of agricultural land and of forest harvesting practices are leading to the encroachment of shrub and forest communities, although globally this process does not compensate for deforestation. Natural forest regeneration in marginal agricultural land and forest maturation represent an opportunity for the recovery of forest-dwelling species, as has been shown for birds (e.g., Gil-Tena et al. 2009, Preiss et al. 1997, Sirami et al. 2008). Moreover, reforested and more mature patches are expected to improve the connectivity among natural or seminatural forests. (For more discussion of connectivity, see Sect. 7.2.2.) In contrast, open-habitat species tend to disappear from abandoned agricultural landscapes as ecological succession occurs and openings disappear (e.g., Moreira and Russo 2007, Sirami et al. 2010), and farmland specialists are particularly vulnerable to this land-use change (Sirami et al. 2010). These changes might therefore be negatively affecting those species that are associated with the historical agriculture–forest mosaic (Blondel and Aronson 1999, Katoh et al. 2009, Scarascia-Mugnozza et al. 2000); in regions such as the Mediterranean, this mosaic hosts a significant portion of the endemic wildlife.

7.3.3   Climate change

Human-driven climate change during the twentieth century has already induced broad biological changes and represents a looming threat for biodiversity (Parmesan and Yohe 2003, Root et al. 2003), but to date, these changes have been small compared to those that have been driven by habitat loss (Parmesan and Yohe 2003). The global average tendency toward increased warming is projected to trigger the displacement of species ranges poleward in latitude or upward in elevation in response to the need of species for suitable climatic conditions. This rearrangement of species distributions has important implications. The dynamics of populations that inhabit the latitudinal margins of a species' range will be critical for its fate (Hampe and Petit 2005). For instance, northern populations of boreal forest species are projected to move into the Arctic tundra (Pereira et al. 2010), although some boreal tree species may be unlikely to find new areas with suitable conditions and will subsequently exhibit contraction of their range (Thuiller et al. 2006). As for populations that inhabit the low-latitude margins of a species' range, global niche-based models forecast a bleak future. However, in mountainous regions, many low-altitude populations may be able to persist through altitudinal shifts, as has been documented for many species during the Pleistocene (Bush et al. 2004, Hampe and Petit 2005); this will not be possible, however, for many high-altitude populations. In the case of tropical forest species, concern has been raised about the absence of species that are able to replace those species currently distributed in tropical lowlands given that these species are already living near the thermal optimum of their functional niche (Colwell et al. 2008). Finally, movements of a species up altitudinal gradients may also result in declines in population sizes, because the area of an altitudinal band diminishes with increasing elevation because of the typical conical shape of a mountain. (The species richness–area relationship is discussed in Sect. 7.2.1.)

   Bioclimatic envelope models (niche-based models) have been used to assess the impact of climate change on biodiversity (Heikkinen et al. 2006). Projected range contractions combined with empirical species–area relationships, which are also used to predict the impact of deforestation (Sect. 7.3.1), have provided scenarios of the future potential extinction risk that is attributable to climate change (e.g., Thomas et al. 2004). But apart from the direct physiological constraints of projected warmer temperatures and protracted drought, the decline in overwinter mortality of some insects (e.g., Hódar et al. 2003, Kurz et al. 2008) and the weakening of some organisms by these constraints (Breshears et al. 2005, Pounds et al. 1999) may result in mass-mortality events (e.g., insect or disease epidemics). However, other aspects of vulnerability such as the sensitivity or adaptive capacity of a species should be considered apart from its exposure to climate change (Dawson et al. 2011). For example, phenotypic plasticity in response to climate change has already been reported for many species (Parmesan and Yohe 2003, Root et al. 2003), and the potential for microevolution may allow adaptation to new climatic conditions (Dawson et al. 2011, Malhi et al. 2008).

7.3.4 Forest fires

The implications of ongoing changes in forest fire regimes for biodiversity differ markedly among regions in the world because of differences in the type of fire regimes under which forest communities have evolved (Sousa 1984). For example, fire-prone forests such as those in the Mediterranean region have been subjected to the selection pressure of fire disturbance for millions of years, thus favoring the evolution of adaptive traits such as serotinous cones and high resprouting capacity (Lavorel 1999). In contrast, in tropical moist forests, fires have been a weak evolutionary force (Barlow and Peres 2004) and they are only recently becoming common due to a combination of climate change and human-induced ignitions (Malhi et al. 2009). The lack of fire adaptation by many tropical tree species may decrease their chances of survival if fire frequency increases (Malhi et al. 2008, 2009).

The dynamic equilibrium in the fire disturbance and succession cycle of fire-prone forests can be disrupted when a threshold of fire intensity, frequency, duration, or extent is exceeded. If this happens, disturbances can carry ecosystems into a different stable domain (Beisner et al. 2003, Holling 1973). In this context, the Mediterranean region's current tendency toward increasing fire frequency and extent (Pausas 2004) may compromise the persistence of fire-vulnerable species, and trigger different successional pathways, ultimately changing the structure and composition of the regional forest ecosystems (e.g., Pausas et al. 2004). For instance, short intervals between consecutive fire events (e.g., in the Mediterranean Basin) might prevent the regeneration of long-lived species with long prereproductive cycles (Whelan et al. 2002). Conversely, long intervals, which are more frequently found in North America, may limit species that rely on fire disturbance for their reproduction. Fire frequency also determines other structural aspects such as the presence of deep litter, logs, or cavities in trees, which are essential for many animal species (Driscoll et al. 2010). Fire extent is also an issue because small to medium fires may promote landscape heterogeneity, which might allow the coexistence of species with different tolerances of fire disturbance, those typical of different successional stages, or both (Moreira and Russo 2007). (See Sect. 7.2.4 for more discussion of the effects of heterogeneity.)

7.3.5 Plantation forests

The increased worldwide demand for wood products and the growing public concern over the loss or degradation of forests are the major causes of a steady increase in plantation establishment throughout most regions of the world, especially in China (FAO 2007). Recent research has shown that planted forests are usually species poor compared with natural forests (e.g., Armstrong and van Hensbergen 1996, Lindenmayer and Hobbs 2004, Moore and Allen 1999), which is attributable both to the decision to plant monocultures and to the lower structural complexity of the

plantations (Brockerhoff et al. 2008); forests with more complex structures support more species by increasing the diversity of niches (e.g., Brokaw and Lent 1999, Ishii et al. 2004).

However, forest plantations encompass a wide range of positive and negative effects on biodiversity, depending on considerations such as the land use being replaced, type of management practices, time since plantation establishment, and landscape context (Brockerhoff et al. 2008). Although plantations have a negative impact on biodiversity when they replace natural forest or non-forest ecosystems, they can contribute to native biodiversity conservation when they replace agricultural land or other intensive land uses. (See Sect. 7.4 for more discussion of this point.) In addition, the conservation value of plantation forests varies broadly as a function of the management practices. Decisions about planting native or exotic timber species, mixed species versus monocultures, the method of land preparation, the abundance of biological legacies (e.g., seed banks, advance reproduction, and vegetative reproductive organs), and rotation length can imply very different scenarios for biodiversity conservation. The structural and compositional characteristics of planted forests can approach, with time, those of other more natural stands, so that they may be able to harbor a large portion of the biodiversity found in those reference natural forests, particularly when appropriate management measures, oriented to habitat quality restoration rather than to intensive timber production, are adopted. Finally, it should be noted that plantation forests can indirectly help biodiversity by satisfying enough of the demand for forest products, so that they alleviate the pressure for more intensive management of the remaining areas of natural forest, which potentially have a higher conservation value.

7.3.6 *Management of adjacent non-forest lands*

Agricultural land-use intensity is a decisive modulator of the degree of impact that deforestation, fragmentation, or habitat degradation has on forest biodiversity (Ewers and Didham 2006, Kupfer et al. 2006). The dramatic and widespread intensification of agriculture is creating landscapes with sharp contrasts between forests and other land uses in terms of ecosystem structure and microclimate. This intensive land use may constitute a filter for the movement of most forest-dwelling species, whereas less-disturbed non-forested lands surrounding forests can be experienced as permeable by many species, with the consequent beneficial effects of increased connectivity (Sect. 7.2.2). In addition, this contrast is expected to preclude forest organisms in deforested or degraded landscapes from supplementing or complementing their habitats or resources, such as food or shelter (See Sect. 7.2.5 for a discussion of complementation and supplementation from cover types surrounding a forest habitat.). Adverse edge effects could also be mitigated by more sustainable land use in the areas surrounding forest habitats, such as the creation of "softer" edges, with a less drastic transition between ecosystem types. Therefore, the detrimental effects on forest biodiversity of deforestation and fragmentation may be exacerbated by land-use intensification.

7.3.7   Forest stand management

In some regions, the increasing demand for wood products is leading to increased exploitation through timber extraction. Silvicultural disturbances can alter the composition of forest communities and trigger succession dynamics, but their exact impact on species diversity will depend on the frequency, intensity, extent, and duration of the disturbance and on how these factors interact with the characteristics of local species. The response of forest communities to the release of resources (primarily sunlight, water, and nutrients) after harvesting will also depend on the overall levels of resources in the system (Kondoh 2001); that is, the same practice will affect forest biodiversity differently on sites with different productivity (Martín-Queller et al. 2013). Despite these idiosyncrasies, some management practices have been found to benefit the species richness of vascular plants (Paillet et al. 2010a, Torras and Saura 2008). This phenomenon might be explained by the "intermediate disturbance" hypothesis (Connell 1978, Shea et al. 2004), which predicts that the maximum species richness will occur at intermediate disturbance levels. At intermediate levels, plants typical of early successional stages and their associated fauna can survive in canopy gaps and coexist with some shade-tolerant species (Shea et al. 2004). Furthermore, enhancing diversity in the overstory will promote microhabitat heterogeneity that will positively influence diversity of many other organisms that inhabit the forest (e.g., Gil-Tena et al. 2007, Kissling et al. 2008, Sobek et al. 2009, Vesseby et al. 2002). Nonetheless, what is an intermediate disturbance for some species may be severe for others and, therefore, mature, unmanaged stands are essential for the maintenance of species diversity of many organisms. (See Sect. 7.2.3 for more discussion of the effects of habitat quality.) This explains the decline of species richness of bryophytes, lichens, and saproxylic fungi in managed forests compared to unmanaged forests; see Paillet et al. (2010a, b) and Halme et al. (2010) for a review of the effects of forest management on the species richness of different taxonomic groups.

From a landscape perspective, ecological succession in forest communities is continuously fed by colonists from neighboring communities at different stages of the cycle or from different habitats ("metacommunity dynamics"; Leibold et al. 2004). Colonization by species adapted to the conditions in a particular stage of succession will depend on the presence of relatively nearby communities that are in similar stages or that are inhabiting habitat with similar conditions. Therefore, an extensive application of the same type of silvicultural treatments throughout the landscape may result in homogenization of the successional stages, and this may (for instance) hinder the persistence of more demanding shade-tolerant species. The reduction in the exchange of species among communities at different stages may also eventually reduce species richness in each local community (e.g., Martín-Queller and Saura 2013). These considerations emphasize the importance of widening the spatiotemporal scope when evaluating the consequences of any silvicultural operation on local species richness. If we are to protect or restore species richness in a forest, we must have an integral view of the whole span of successional stages in that forest and of the neighboring communities upon which persistence of

some species may depend in the long term. Indeed, it may be inappropriate to focus on the biodiversity of an individual forest if doing so leads us to ignore the successional processes at a landscape scale that will naturally and eventually recreate that biodiversity elsewhere in the landscape. The preservation of unmanaged forests intermingled with managed stands in the landscape will help to ensure the persistence of disturbance-sensitive species, while providing sources for recolonization of disturbed sites by species that require disturbance during the successional cycle. In addition, an appropriate infrastructure of dispersal vectors must be assured by, for instance, avoiding excessive removal of the forest understory, since seed-dispersing birds will be attracted by an abundance of fruiting shrubs (García et al. 2010, Tellería et al. 2005). Similarly, the promotion of forest connectivity for mammals may attract species that disperse seeds via zoochory (e.g., Minor and Lookingbill 2010).

7.3.8   Invasive species

Invasive species are exotic species that establish and proliferate to the detriment of native species and ecosystems; however, they represent only a small portion of the larger number of naturalized exotic species (Mack et al. 2000). Although invasions are not a novel phenomenon, they are currently considered to be an important agent of global biodiversity change because of their unprecedentedly large geographical scale and the number and frequency of invasions (Ricciardi 2007). Invasive species have contributed to many animal extinctions in the last few 100 years (Clavero and García-Berthou 2005), with a particularly relevant role in the case of birds on oceanic islands (Blackburn et al. 2004, Sax et al. 2002). Extinctions are the extreme case of biodiversity loss; however, some authors point to the role of species invasions in global biotic homogenization (e.g., Sax and Gaines 2008). Even if exotic species increase local species richness, they are generally cosmopolitan species and do nothing to favor biodiversity at larger scales.

Examples of the negative consequences of species invasions on forest biota are numerous. Dramatic reductions of the population of a species can result from species invasions, as was the case during the destruction of almost all American chestnut (*Castanea dentata*) within their natural range by a fungus transported in imported exotic Asian chestnut (Mack et al. 2000). Another significant example is how the invasion of planted trees (*Pinus* and *Acacia* spp.) into the South African fynbos (native shrubland) transformed this endemic-rich ecosystem due to changes in water availability for native species (Richardson and van Wilgen 2004). Species invasions can also alter the functioning of forest trophic chains, as was observed in New Zealand with the invasion of two wasp species into southern beech (*Fagus* spp.) forests (see Mack et al. 2000 for this and other examples).

Because human-driven disturbances generally increase the invasion by exotic species (Alpert et al. 2000, Lozon and MacIsaac 1997), habitat loss or degradation usually act synergistically with species invasions to create a loss of biodiversity

(Didham et al. 2007). Furthermore, the invasibility of a forest community is influenced by the configuration and the composition of the surrounding landscape (see Vilà and Ibáñez (2011) and the references therein). For example, increased forest edge length in fragmented landscapes, logging roads, or subsidies from a highly disturbed matrix (see complementation and supplementation processes in Sect. 7.2.5.2), can all increase the risk of exotic species invasions in forest interiors (Didham et al. 2007, Kupfer et al. 2006, Vilà and Ibáñez 2011).

7.3.9   Interactions and synergies among different processes

Although we have presented a series of processes as if they act separately, any realistic scenario will be characterized by the interactions among these processes, frequently with synergistic effects (Brook et al. 2008). For example, the impact of fire in tropical forests is influenced by logging and fragmentation, which increase the flammability of tropical forests by drying the understory in canopy gaps and by greatly increasing the amount of dry, fire-prone forest edges and woody debris (Bradshaw et al. 2009b, Lindenmayer 2010). A greater length of forest edges also increases the probability of ignition. This logging–fragmentation–fire interaction is enhanced by severe droughts, whether natural and episodic or induced by global warming (Malhi et al. 2008). In contrast, in Mediterranean forests, increased continuity in the flammable area is being caused by rural abandonment; coupled with climate change, this may exacerbate the size and severity of wildfires. Small to medium wildfires, however, could compensate for the homogenization of the landscape derived from land abandonment by promoting heterogeneity (Loepfe et al. 2010). (See Sect. 7.2.4 for a discussion of the effects of heterogeneity.)

The impact of climate change also results from its interaction with the other agents discussed in this chapter. For example, the capability of a species to adjust its range to keep pace with high rates of climate change depends on its dispersal ability, on the availability of necessary resources in the new habitats, and on landscape permeability. In fact, for a given period, estimated distance shifts in temperature isoclines in some regions may be substantially higher than the estimated maximum dispersal distances of some species (Bacles and Jump 2011). This means that spatial discontinuities (range-shift gaps) between current and projected areas with suitable climatic conditions may preclude some species from shifting their ranges, which is especially likely in the tropics (Colwell et al. 2008). This shift will be curtailed by a reduced functional connectivity as forest landscapes become more degraded, fragmented, and subject to intensified land use (Brook et al. 2008, Colwell et al. 2008). For a species to reach new, climatically suitable habitats may therefore require "assisted migration", a complex and controversial topic that is discussed in Chap. 2 of this book. However, successful shifts in the distribution of a species may also indirectly promote tree mortality by leading to a higher prevalence of diseases due to habitat overlap between species that were formerly separated (Bradshaw et al. 2009a).

Although the complexity of these interactions and of others, some of which are discussed throughout this chapter, hinders our ability to predict the future impacts of landscape changes on the biodiversity of forest ecosystems, conservation policies focusing on single, separated processes will clearly be ineffective and should be avoided.

7.4 Conclusions and general recommendations for mitigating the impacts of landscape change on forest biodiversity

The complexity of landscape change and the uniqueness of every landscape and species make it impossible to offer a comprehensive set of management guidelines, but we can recommend some general principles that will be broadly relevant. We will start with a fundamental idea that may risk stating the obvious: maintaining or restoring forest cover will favor the abundance and richness of forest-dwelling species, and this will foster resilience in the context of landscape change. It is tempting just to say "the more forest, the better", but the real situation is not that simple. The portion of the landscape that needs to be covered by forest to sustain a population of a given species will vary greatly among species depending on their area requirements. (See the concept of "minimum viable population" (or metapopulation) in Sect. 7.2.1.) It is also important to recognize that the habitat needs of species that require other types of vegetation, notably grasslands, also constrain the idea that "more forest is better for biodiversity", especially in the context of afforestation. (See, for example, the responses of generalist species in Sect. 7.2.5.) One could ask, "Is there a minimum threshold for the amount of forest in a landscape?", but again, this is a species-specific question. To take an extreme example, some species might find habitat, or a key habitat element (e.g., a nest site), in a single tree.

Almost as important as the total area of forest is its spatial distribution. A landscape dominated by a large, contiguous tract of forest may provide optimal habitat for species whose survival is limited in small areas, but other species may thrive in a landscape of scattered forest patches, especially if they can move readily among patches and perhaps form metapopulations. (See Sects. 7.2.1 and 7.2.2 for a discussion of metapopulation dynamics and connectivity.) Species that are associated with edge environments—habitats at the interface between forests and other types of ecosystems—may also find superior habitat in a landscape of small, irregularly shaped patches.

Spatial distribution is important because it is a primary determinant of connectivity, which is measured largely by the ability of species to move across a landscape. Mobility is obviously important to species such as a carnivore that must travel widely to find sufficient food, but ultimately it is important to all species because of its effect on processes such as gene flow and the shifting of geographic ranges in response to climate change. Some forest species can move across a fragmented landscape by using forest patches as stepping stones, but open areas are strong filters for other species, and may even function as barriers to their movements.

Such species may be able to move using linear strips of forest such as the riparian forests that line many rivers or along the hedgerows that persist between agricultural fields.

One could argue that a landscape mosaic of numerous differentiated forest patches might be more resilient against change, as exemplified by the folk wisdom, "don't put all your eggs in one basket". For example, an isolated patch might be less likely to burn in a landscape-scale fire. However, as a generalization, the fact that most natural forest landscapes have a high degree of connectivity suggests that connectivity will generally improve resilience against change, by (for example) allowing species to recolonize sites following a local extinction event.

To summarize the previous paragraphs, having extensive forests that are well connected is fundamental to conserving forest biodiversity. In well-forested landscapes, this will require maintaining existing stands and minimizing fragmentation by roads and perforation by the conversion of patches into other land uses. In landscapes that have lost substantial forest cover, this will require forest restoration, undertaken with a particular focus on restoring connectivity by placing new forests in strategic locations such as along riparian zones or as a series of stepping stones that can maintain species fluxes between distant blocks of forest. (See Sect. 7.2.2 for a discussion of connectivity.)

In addition to the quantity and distribution of forests, managers must consider their quality (Sect. 7.2.3). From a biodiversity perspective, the most valuable forests are likely to be pristine, old-growth forests for two primary reasons: First, such forests are rare in most parts of the world and are thus likely to provide habitat for species that are absent or uncommon elsewhere. Second, old forests typically have features such as a sizable accumulation of biomass, high vertical diversity, and canopy gaps that let them support more species than other forest types. Conserving these forests is straightforward, at least conceptually; it requires identifying them and protecting them in a reserve system that is large enough to accommodate the natural dynamics of disturbance and succession.

Most forests are unlikely to be set aside because human demand for timber and other forest products dictate that they will be actively used. Fortunately, it is possible to extract timber in a manner that will sustain biodiversity with relatively modest compromises. There are two key paradigms for maintaining biodiversity in forests that are being managed for timber production (Hunter and Schmiegelow 2011). "Using nature's template" ("emulating natural disturbance") recognizes the coarse similarity between logging and natural forms of disturbance that kill trees and initiate secondary succession, and is based on designing silvicultural systems that will emulate natural disturbances to the extent that is feasible. The key idea is that if species have evolved to survive and even thrive in response to certain natural disturbances, then anthropogenic disturbances will have less impact (but certainly not zero impact) if they closely resemble these natural disturbances. For example, if fires have a return interval of 100 to 200 years in a particular type of forest, then a logging cycle of 100 to 200 years will have less impact than 1 of 50 years. A second paradigm for maintaining biodiversity in managed forests—"diversity begets diversity"—simply recognizes that a diverse forest landscape with stands of many

ages, sizes, and tree species compositions will provide habitat for a greater array of species than a highly uniform forest. Such a forest landscape would probably also be more resilient against change agents than a uniform forest.

Plantation forests are widely seen as impoverished from a biodiversity perspective, and there is some truth to that generalization. However, there are some important caveats to note. First, some species, including some uncommon ones that are of concern to conservationists, such as the New Zealand falcon (*Falco novaeseelandiae*), find suitable habitat in plantations. Second, plantations probably constitute suitable temporary habitat for many dispersing organisms. Certainly, they are likely to be preferable habitat compared to wheat fields or parking lots. Thus, establishing plantations provides an important opportunity to restore connectivity by placing them between existing forests. Third, by producing large volumes of timber from a relatively small area, plantations can remove some of the pressure for timber production from natural and seminatural forests, thereby allowing them to be managed for biodiversity. Fourth, some species naturally grow in relatively homogeneous ecosystems, such as the fire-based jack pine (*Pinus banksiana*) ecosystems of boreal Canada. Although such ecosystems are typically more diverse than plantations, the similarity is closer than it is for more diverse ecosystems.

In short, maintaining forest biodiversity in the face of a complex suite of disturbance factors will be most likely to succeed if we can maintain landscapes of well-connected, extensive, and high-quality forests. This is a simple goal to articulate but a challenging one to implement. Ideally, a significant portion of these forests will be set aside in old-growth reserves, and the balance will be managed for both timber production and biodiversity conservation through the careful application of silvicultural techniques that are minimally disruptive and that maintain a diversity of forest conditions. Change is inevitable, but such a landscape will be quite resilient against undesirable change from a biodiversity perspective.

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