

‘Ecological land-use complementation’ for building resilience in urban ecosystems

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Abstract

Few scientific analyses exist on how different land uses can be configured for greater support of biodiversity and ecosystem services. Based on ecological premises, and through a synthesis of information derived from the literature related to urban ecology, this paper elaborates on the potential biodiversity benefits of ‘ecological land-use complementation’ (ELC). The approach builds on the idea that land uses in urban green areas could synergistically interact to support biodiversity when clustered together in different combinations. As proposed, ELC may not only provide for increased habitat availability for species, but also promote landscape complementation/supplementation functions and other critical ecosystem processes; hence, realize ‘emergent’ ecological functions of land use. Planners and urban designers could adopt ELC to promote ecosystem resilience when planning new urban areas, such as in the support of ‘response diversity’ among functional species groups, and in the support of ecosystem services. ELC-structures in urban landscapes could also be used as arenas to promote participatory management approaches and Local Agenda 21. The paper concludes by summarizing some guiding principles for urban planning and design.
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1. Introduction

Urban ecosystems are the most complex mosaics of vegetative land cover and multiple land uses of any landscape (Foresman et al., 1997). Urban land uses are in a state of continuous flux, where change is the norm rather than the exception. Although decisions governing land-use change almost exclusively occur at the local level (Theobald et al., 2000), such change may be driven by non-local drivers that cannot be anticipated in advance (Altieri et al., 1999). Throughout the dynamic transformation of land use, less desirable, unwanted states may be witnessed in urban areas, such as when the biota increasingly is lost due to habitat degradation, fragmentation and loss, with the subsequent loss and thinning out of ecosystem services. Such ‘benefits that people obtain from ecosystems’ include provisioning services (the products obtained from ecosystems); regulating services (the benefits obtained from the regulation of ecosystem processes); cultural services (the nonmaterial benefits people

obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences); and the supporting services (those that are necessary for the production of all other ecosystem services) (MA, 2005).

The loss of such services also leads to loss of ecosystem resilience and options for future generations (Folke et al., 2004). Although the concept of resilience holds different meanings to scientists (Folke, *in press*), it is used here as the capacity of an ecosystem to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity and feedbacks (Berkes et al., 2003; Carpenter and Folke, 2006; Holling, 1973). This also includes an ecosystem’s capacity to recover from management mistakes (Fischer et al., 2006).

Resilience building should be part of the agenda of urban spatial planning and design. To date, urban development generates some of the greatest local extinction rates of species and frequently eradicates a large proportion of native flora and fauna (McKinney, 2002). Land use in urban areas has also a particularly strong influence on biodiversity, and will likely have the largest effect on terrestrial ecosystems in the coming century (Sala et al., 2000). As recent studies of satellite data indicate (Hansen et al., 2004), land use continues to intensify in formerly

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occupied areas (e.g., urban areas) often with an overlap of location of areas rich in biodiversity (Ricketts and Imhoff, 2003). Humans tend to settle in areas with high ecosystem productivity with people most dense on lands suitable for agriculture or in low elevation and coastal areas that also support high levels of biodiversity (Hansen et al., 2004; Ricketts and Imhoff, 2003).

There is much to be gained from building in ecological functions in the accommodation of land uses in the future growth of cities. This, however, requires a much stronger partnership among ecologists, urban designers, landscape architects, and urban residents than has hitherto been the case and more knowledge about the functioning of urban ecosystems needs to be developed (Felson and Pickett, 2005). While much is known about the interactions between land-use change and biodiversity at the global level, little analysis exists on how varying landscape designs influence landscape functions in specific contexts (e.g., Hobbs, 1993, 1997), and on the synergistic effects that different land uses may have in terms of supporting processes essential for biodiversity. The aim of this paper is therefore to synthesize information on land-use configurations that more optimally support ecosystem processes and promote resilience in urban settings, and to elucidate some guiding principles for urban planning and design.

2. Framework of analysis

2.1. Scope of the paper

Through a review of the ecological literature (mainly urban ecology), this paper focuses on land-use combinations that ecological premises suggest promote biodiversity. Such combinations are here referred to as ‘ecological land-use complementation’ (ELC). This approach builds on the idea that constituent land uses synergistically interact to support biodiversity when clustered together relative to when they are interspersed in a heavily developed urban matrix.

While practitioners may not be implementing as many ecological design structures in landscape architecture as might be expected (Calkins, 2005), it is often the case that local governments are limited by knowledge for how to best maintain biodiversity in urban settings (Sandström et al., 2006). Insights generated in this paper may thus help planners and designers to better plan for biological conservation and management in urban development in congruence with other existing biodiversity management approaches (see, e.g., von Haaren and Reich, 2006).

One merit of ELC is its consideration of both the spatial structure and the fundamental role that ecosystem processes have for the maintenance of biodiversity (e.g., species movement, pollination, and seed dispersal). Normally, practitioners emphasize landscape structure and aesthetic values, but pay less attention to ecosystem processes in landscape designs (Hobbs, 1997; Kendle and Forbes, 1997).

While the ecological premises behind ELC have been described by ecologists as important determinants for biodiversity support in different landscape types, and some have been used in the designation of protected areas, little interest

have been devoted to how those land use types that people use on a more regular basis can be spatially arranged to provide greater biodiversity support. In urban settings, these land types include areas for human habitation, work, education, recreation and amenity. Hence, this paper focuses on ecological land-use complementation that involves different types of urban green patches. In particular, it generates insights on how this approach can contribute to build resilience in urban ecosystems, such as for sustaining ecosystem services—a particularly relevant issue considering that ecosystem services are declining in many parts of the world (MA, 2005). Moreover, ELC can be used to promote ‘response diversity’ which is critical for the maintenance of ecosystem processes. Response diversity refers to the diversity of responses to environmental disturbance among species that contribute to the same ecosystem function (Elmqvist et al., 2003). In addition, because ELC takes into account the critical role of active land management for improving conditions for and qualitative attributes of species, the paper discusses how the approach could be used to promote a wider integration of urban residents in biodiversity management.

The paper begins by outlining the theoretical underpinnings behind ELC. Next, examples of land-use complementation are elaborated on, as synthesized from the ecological literature. These examples are further discussed in conjunction with the applicability of ELC in city-regions. The last section sums up the major insights generated in this paper and provides some general guidelines for urban planning and design.

2.2. Theoretical underpinnings of land-use complementation

Ecological land-use complementation (ELC) draws on the merging of some well-known theoretical concepts in ecology. One such premise is the landscape complementation/supplementation hypothesis developed by Dunning et al. (1992). Accordingly, in a landscape of different patch types, such as in heterogeneous, urban landscapes, a species needs to move between patches to obtain critical amounts of resources, i.e., for foraging, roosting and breeding; hence, an individual uses resources complementally to fulfill different life cycles (Pope et al., 2000). Landscape complementation involves a species requiring at least two different resources provided by habitats within the same season, and that resources are available in close proximity to each other (Eybert et al., 1995). Also, an organism may supplement its resource intake by the use of substitutable resources in different habitats (Quin et al., 2004), such as when birds use ruderal areas as seed sources to supplement those available in agricultural fields (Fuller et al., 2004) (Fig. 1). Hence, both habitat composition and configuration can variously affect the individuals, populations, and communities that inhabit a landscape (Guerry and Hunter, 2002) and patches used to complement/supplement resources can form ecologically functional units (Quin et al., 2004). It has been shown that these processes also occur among species confined to urban ecosystems (Blair, 1996; Melles et al., 2003).

In addition, ecological land-use complementation draws on the island biogeography theory (MacArthur and Wilson, 1967)

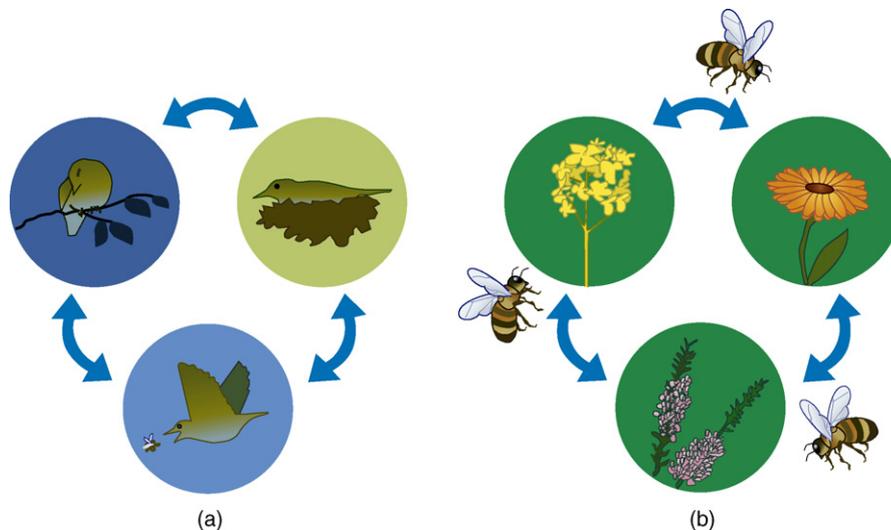


Fig. 1. The two processes of (a) landscape complementation, and (b) landscape supplementation. These processes occur when individuals move between different habitats in the landscape to make use of non-substitutable and substitutable resources, respectively. Landscape complementation highlights the requirement for many species to link together different habitat types to complete their life cycles and is a measure of the proximity of critical habitat types and the degree to which organism can move between them.

in its broadest sense. Accordingly, area is a key determinant for species occurrence and diversity and it is generally assumed that habitat diversity increases with area (Hooper et al., 2002; Simberloff, 1986). Because large islands have more habitat diversity, they hold larger populations, and a greater number of populations (Primack, 1993). For example, findings on woodland fragments suggest that bird species are more likely to become established in larger fragments due to greater habitat/area availability (Hinsley et al., 1995; Villard et al., 1999)—a relationship also applicable to species groups in urban settings (discussed in the next section).

Moreover, proximity of different habitats is an important determinant for biodiversity. Clergeau et al. (2001) showed that local habitat features are more important in urban areas than surrounding landscapes in determining bird species richness, indicating that site-specific actions and in particular management of local variables around larger urban green areas are vital to account for in urban ecosystem management (see also Morimoto et al., 2006). This suggests that species in a patch are likely more affected by the qualitative characteristics of adjacent patches than by those of more distant parts of the landscape (Melles et al., 2003; Rodewald and Yahner, 2001). In addition, the quality of green areas in urban settings is a key determinant for species occurrence and migration patterns (e.g., Hardy and Dennis, 1999; Vandermeer and Carvajal, 2001; Wood and Pullin, 2002), an indication of what role active management plays for improving conditions for species in urban areas.

3. Examples of ecological land-use complementation

3.1. Land-use complementation of urban green patches

Ecological research shows that the species–area relationship is generally applicable for urban ecosystems. For example, this has been shown for plants (Dawe, 1995), amphibians (Cornelis

and Hermy, 2004), birds (Fernandez-Juricic and Jokimäki, 2001; Morimoto et al., 2006), and mammals (Dickman, 1987). Drawing on habitat island research, Fernandez-Juricic and Jokimäki (2001) found a general consistency in the patterns of occupancy among bird communities in city-parks from southern and northern Europe. Park area was the main factor accounting for the probability of park occupation at the community and individual species levels. This relationship can be explained by the area requirements of individual species, associated with the availability of resources (e.g., food, nest sites), higher habitat diversity in large city-parks, higher nest concealment that reduces predation pressure, and processes related to interspecific competition.

In urban planning and design, habitat-enlargement can be achieved through the allocation of different types of urban green patches in close proximity to each other. For example, ecological studies show that domestic gardens often hold high levels of plant diversity (Gaston and Thompson, 2002; Kühn et al., 2004; Maurer et al., 2000; Thompson et al., 2003), correlated to a high invertebrate fauna with native pollinators (Blair, 1996; Gaston and Thompson, 2002; Shapiro, 2002). It has also been shown that residential areas with ample garden areas increase available habitat for species and can act as conduits for wildlife (Barker, 1997; Szacki et al., 1994; Young and Jarvis, 2001). When domestic gardens are located adjacent to city-parks, avian diversity could be promoted through landscape complementation functions provided by local variables such as the presence of native tree cover, berry shrubs, ponds and fresh water sources, which increase the likelihood of attracting sensitive species (Blair, 1996; Melles et al., 2003). Such a ‘binary’ land-use configuration holds a greater proportion of different bird species relative to single, isolated parks in urban areas (Melles et al., 2003; Anne Kinzig, School of Life Sciences, Arizona State University, personal communication, 3 May 2004).

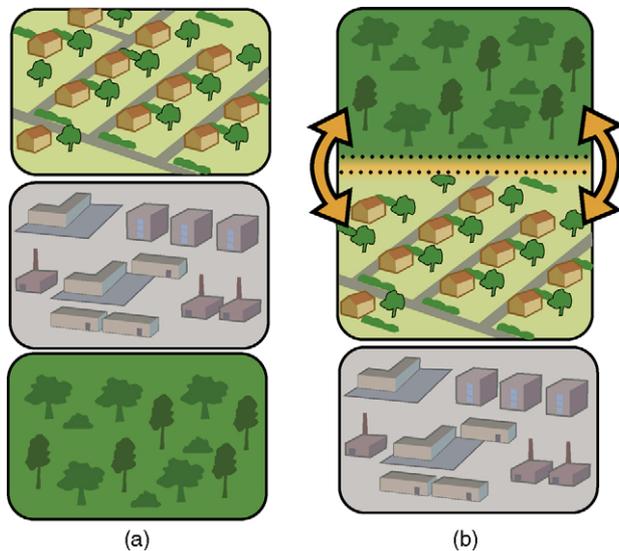


Fig. 2. An example of a ‘binary’ configuration of urban green area patches. Relative to when two green-area patches are located in isolation from each other (situation a), green-area patches located close to each other (situation b), could more optimally provide for landscape complementation and supplementation functions and the support of ecosystem processes, such as seed dispersal and pollination (represented by the arrows). This is especially relevant to consider when the urban matrix constitutes highly developed built-up lands that inhibit species movement. In situation b, the overall diversity of the combined area will also consist of species that can utilize the ecotone between the two green-area patches (represented by the dotted line).

In turn, Chamberlain et al. (2004) suggest that the likelihood of many species occurring in domestic gardens is dependent on the surrounding local habitat rather than the garden habitat alone. It should be recognized that species confined within binary land-use configurations are dependent not just on its size or internal structure but also on complementation and supplementation of resources that in turn provide vital ecosystem processes such as seed dispersal and pollination (Fig. 2). For example, insects with very different habitat requirements at different stages in their life cycles may use domestic gardens when foraging as larvae and use open grasslands of city-parks to forage as adults.

Ecological land-use complementation may involve the clustering together of a whole range of different green patches in cities to increase available habitat and promote ecological processes. Examples include domestic gardens and allotment areas, university campuses, city-parks, golf courses, churchyards, cemeteries, and even wooded streets (Fernández-Juricic, 2001). These land uses often constitute quite extensive areas of cityscapes (Kendle and Forbes, 1997). For example, in and around the city of Stockholm (Sweden), 18% of the total land area constitutes domestic garden habitats and golf courses alone (Colding et al., 2006). Moreover, many universities contain large tracts of green patches that may serve as critical habitat for species. For example, the university campuses in Pune city, India, contain up to half the plant, bird and butterfly species, although only cover-

ing less than 5% of the city’s land area (Kulkarni et al., 2001).

3.2. Land-use complementation and agriculture

A key consideration in all production landscapes is heterogeneity of land uses and land-use intensities (Benton et al., 2003; Fischer et al., 2006). For example, it has been shown that uncropped patches and non-farmland habitats provide nesting, foraging or roosting resources for several declining farmland bird species (Fuller, 2000). Individuals that breed in non-farmland habitats may feed on farmland, and many birds depend on farmland resources outside the breeding season (Fuller et al., 2004; Morimoto et al., 2006). Certain birds may also utilize woodlands for temporary shelter.

Green patches within residential housing and allotment areas provide habitats for birds (Cannon et al., 2005; Chamberlain et al., 2004; Mason, 2000), including farmland species (Bevington, 1991; Summers-Smith, 1999). Many of these birds constitute effective pest-regulators on agricultural cultivars. Hence, these green patches could attract insect-controlling birds and be used to buffer against outbreaks of various pest populations—a particularly important aspect to account for in the resilience building of urban farmlands. Backyard habitats often hold high levels of native pollinators (Cane, 2001), thus housing development involving ample backyard habitats should be considered to a greater extent when it comes to promote pollination of cultivars on urban farmland. Bees of medium body size regularly fly 1–2 km from nest to forage patch, and even longer distance (Cane, 2001; Kremen et al., 2004), suggesting that the designation of residential areas with gardens should ideally be located within this range from crop fields in order to promote pollination.

Golf courses, if managed correctly (Terman, 1997), have also been shown to increase biodiversity when established in agricultural landscapes. Golfing estates often retain different relict landscape types such as heathlands, dune grasslands, and other ancient woodlands that have declined substantially in many parts of the world (Brennan, 1992; Gange, 1999; Green and Marshall, 1987; Yasuda and Koike, 2006). Tanner and Gange (2005) found bird and insect diversity to be significantly higher on golf courses than on adjacent agricultural land, with a higher proportion of insect feeding birds and a significant relationship between bird diversity and tree diversity. Golf courses also often hold wetland habitats such as ponds (Dair and Schofield, 1990; Rosenzweig, 2003; Colding et al., 2006) that largely have been lost on farmlands (Williams et al., 2003). Ponds on many Swedish golf courses support declining farmland birds and amphibians (Colding et al., 2006). Moreover, Tanner and Gange (2005) found golf courses to contain a higher diversity and abundance of both ground beetles (Carabidae) and bumblebees (Hymenoptera, Apidae) relative to adjacent farmland. Carabid species are recognized as vital omnivorous predators on arable fields, providing farmers with a natural, self-regulating pest control. As these examples suggest, planners could contribute to make agriculture more sustainable in urban areas through a greater consideration of land-use complementation.

3.3. ELC as an alternative to smaller nature reserves

Due to limits of available space for their designation, many nature-protected areas in urban settings follow political jurisdictional boundaries rather than biogeographic ones. Hence, such reserves poorly account for critical ecosystem processes, species ranges, and even anthropogenic considerations (Ricketts and Imhoff, 2003). Also, urban reserves are often too small and isolated within a matrix dominated by either agriculture or urban development, which is a contributing factor in the gradual loss of species in these reserves (Drayton and Primack, 1996). Smaller protected areas often lack key resources needed by species (Savard et al., 2000), suggesting that the types and extent of surrounding land uses are especially critical to account for when it comes to biodiversity conservation in cities (Flores et al., 1998; Rodewald and Yahner, 2001).

Planners and urban designers should therefore consider how land use in urban settings could optimally serve as ‘buffers’ around patches of natural habitats. This approach has been adopted in Biosphere Reserves (McNeely et al., 1990) and Ecological Networks (Bennett, 2004), although at much larger spatial scales. Buffers are particularly important where surrounding land exerts highly negative influences on sensitive areas, e.g., providing a source of invasive species or chemical pollutants (Fischer et al., 2006). For example, in and around the city of Stockholm, Sweden, nearly one-fifth of all golf courses are located in direct adjacency to nature reserves, serving as buffer zones to these (Colding et al., 2006). A median-sized Swedish nature reserve constitutes only some 20 ha of land, so the additional habitat provided by a median-sized Swedish golf course of some 60 ha provides substantial habitat availability for species confined to smaller reserves. Considering that roughly 70% of a golf course constitutes non-playable natural areas, such as smaller hillside patches, wetlands, stream banks, grasslands, groves and woodlands, golf courses could increasingly become an environmental asset in urban settings if they are designed and managed correctly (Colding et al., 2006).

Buffer habitats may not only promote landscape-level processes (Wiens, 1997), but the added value of active management of constituent buffers could contribute to build resilience for species confined to reserves or other natural areas, such as urban woodlands (Morimoto et al., 2006). For example, because landholders adopt different management practices on their lands, critical resources confined to buffers could be used by species in nature reserves during times of natural disturbance. In Australia both kangaroos and wallabies retreat to urban gardens in times of drought and fire to find suitable foraging habitats since gardens are irrigated and actively nurtured. These mammals may hence survive the disturbance, and later on when normal conditions resolve, re-colonize natural areas again. Another example is reported by Gwyn (2002) where local gardeners by way of the deliberate planting of exotic oaks and other fruit trees on their lands, provide foraging resources to Jay populations at times when the native acorn crop in the surrounding and protected oak woodlands fails. Through this management practice, local gardeners promote natural oak forest regeneration through their support of Jays, which are known to be key dispersers of

acorns (Hougnier et al., 2006). Such complementary functions of land uses that build resilience in ecosystems should be more widely considered in urban design and biodiversity conservation planning.

4. Discussion

As suggested by the examples presented above, ecological land-use complementation may not only increase habitat-availability for species confined to urban areas, but also promote landscape complementation/supplementation functions that in turn nurture species movement, facilitating key ecosystem processes such as pollination and seed dispersal. Hence, ELC-structures may promote ecosystem functions of one or several land use types that are not provided for when these are located as single, isolated units. For example, a golf course holding freshwater ponds of potential habitats for wetland dependent organisms but hosting few forest patches may have little chance to sustain these organisms by itself when the surrounding landscape constitutes built-up lands. However, when such a course is located adjacent to a natural area with forest habitats, landscape complementation is provided for. Groups such as amphibians and macroinvertebrates can use these binary structures to complete their different life cycles, e.g., for breeding foraging, and over-wintering. Hence, ‘emergent’ ecosystem functions of a land use may be realized by adopting ELC in landscape design and species conservation, and land uses contained within such structures could better serve as environmental assets in urban landscapes (Fig. 3a).

ELC may also promote ‘response diversity’. For example, through the allocation of neighborhood areas with ample garden habitats in close proximity to crop fields, increased resource availability for a greater number of native pollinators is provided for; hence, response diversity for this functional group is promoted (Fig. 3b). This in turn insures against various negative consequences, such as the Varroa mite infestation in honeybee colonies (*Apis mellifera*) that may greatly inhibit pollination in many parts of the world. Management of many species within a single functional group promotes resilience by reducing the risk of a specific ecosystem function being entirely lost from a landscape (Elmqvist et al., 2003). This means that if honeybees are affected by a potential natural disturbance, other pollinator species may take over the role of pollination.

4.1. Critical considerations of ELC

While ELC can contribute to build resilience in urban ecosystems, there might be situations where land-use complementation could lead to undesirable biodiversity outcomes. For example, private gardens in Florida have been shown to harbor pests with severe economic repercussions in the agricultural sector (Pers. Com., Lance Gunderson, Emory University, Atlanta). Hence, it is critical to assess what role pest species and invasive species have when adopting ELC-designs. To what extent exotic species contribute to reduce or enhance the generation of ecosystem services is virtually unknown for any urban area; however, because introduced species make up a large proportion of the urban

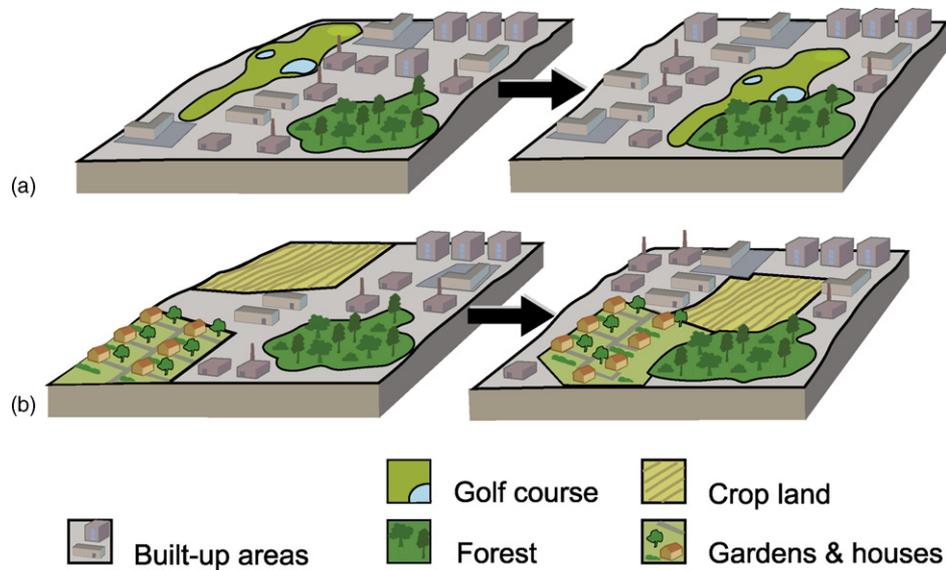


Fig. 3. 'Emergent' ecological functions provided through land-use complementation. In (a) a golf course with ponds with no forest patches could serve as suitable breeding-habitats for amphibians when located adjacent to a forest habitat due to landscape complementation. Similarly, in (b) when urban gardens are clustered adjacent to forest patches and crop fields, pollinators may be promoted. Different pollinators may use gardens for collecting pollen and nectar resources, use adjacent forest habitats as nesting sites, and perform important pollination of food cultivars on adjacent crop fields. In this case, such a configuration could promote 'response diversity' to environmental stresses among pollinators.

biota, it is important to assess not only to what degree they are detrimental, but also to what extent they may enhance local diversity and maintain important processes in urban ecosystems (Elmqvist et al., *in press*).

In some situations land uses should also by necessity be kept apart. For instance, in some cities where air pollution loads are high, it may be unwise to locate further urban development close to agricultural areas to minimize risks of exposing food cultivars to additional pollutants. Potential leakage of pesticides and fertilizers from agricultural fields, and even from golf courses, to surface water and groundwater of adjacent ecosystems (Cohen et al., 1990), may also restrict the applicability of ELC in some cases. In addition, many species groups exist as metapopulations (Hanski and Gilpin, 1991; Hanski, 1998) and need urban green patches as 'stepping stones' and corridors for species movement and for genetic exchange over wider temporal and spatial scales (Simberloff and Cox, 1987). Hence, ELC as a conservation approach should not be used in isolation, but needs to take into account the distribution-pattern of other existing green structures in the urban landscape. Generally, a more detailed knowledge about the functioning and behavior of species in city-regions will benefit the development of ELC at local levels. The sections below outline areas in which ELC may be particularly useful for planners and urban designers to adopt.

4.2. ELC in the planning and design of new urban land uses

While ELC may be used in the redesign and modification of already developed urban core areas, it is not easy to enlarge existing urban green patches (Fernandez-Juricic and Jokimäki, 2001). Instead, much of current urban growth takes place in the suburbs (McKinney, 2002). Urban biodiversity usually also peaks at this scale of the cityscape, where species tend to be 'urban adapters'

(Blair, 2001), adapted to forest edges and adjacent open lands. Animals within this category exploit many resources, including human-subsidized foods (McKinney, 2002). Such species are also less sensitive to the presence of humans and pets. Opportunity for urban designers to adopt ELC is therefore likely greatest at this level, for example, when development of new housing and associated real estates are to take place, or when the designation of a new neighborhood park, university campus, or a golf course are considered.

At this scale of the cityscape, it might be useful also to take into account how publicly and privately managed lands could complement one another to better support biodiversity. Oftentimes, governmentally managed lands are susceptible to economic fluctuations, such as in London where the local authority expenditures for the maintenance of city-parks and protected areas decline in years when local government is under pressure (Greater London Authority, 2001). This indeed affects the quality of management since there is a positive correlation between funding and management capability. In contrast, privately managed land types (e.g., private domestic gardens) are less sensitive to economic fluctuation because management is voluntary-based and conducted for human recreation (Oldfield et al., 2003). Hence, ecological land-use complementation that involves both publicly and privately managed land types may contribute to level out some adverse effects in terms of management inputs during periods of economic recession.

When urban growth occurs in the rural parts of the cityscape, ELC could also be explicitly adopted for the design of 'conservation targets' to support ecosystem services, such as pollination and pest-regulation that are crucial for sustainable agriculture (Naylor and Ehrlich, 1997; Kremen et al., 2004). Alternatively, ELC could be used to support seed dispersing birds that may structure species composition in forests, such as the Eurasian

Jay (*Garrulus glandarius*) that is critical for natural oak forest renewal (Hougnier et al., 2006). Considering that ecosystem services are declining in many parts of the world (MA, 2005), urban planners need to consider to a greater extent designs that support the generation of ecosystem services in the process of urbanization.

4.3. ELC as arenas for ‘designed experiments’ and ‘adaptive co-management’

It should be emphasized that land-use complementarities already exist to a higher or lesser degree in most landscapes. Such structures could be detected and further analyzed through remote sensing techniques, e.g., Geographic Information System(s) (GIS). Given the potential inherent biodiversity values of such structures, these could serve as arenas for ‘designed experiments’ to improve ecological functions in cities (sensu Felson and Pickett, 2005). For example, they could be managed in ways that improve species richness and ecological processes, or to promote ‘focal species’, which are known to have broad-scale ecosystem effects and include species considered keystones and umbrella species (Bani et al., 2002; Dale et al., 2000) as well as ‘mobile link species’ that transfer matter and energy across trophic levels or link ecosystems over space (Lundberg and Moberg, 2003). Similar to the approach taken in ‘wildlife gardening’ (Baines, 2000), the management goal of such structures could be to find the missing components in the landscape that will best meet the needs of focal species.

Because ELC-structures are managed by different landholders and green-area user groups (e.g., community neighborhood groups, gardeners of horticulture clubs, allotment associations, green keepers of golf clubs, farmers, and various governmental maintenance staffs), they represent areas where participatory management approaches could be developed. One such approach is adaptive co-management, tailored to specific places and situations and supported by, and working with, various organizations at different levels in society (Folke et al., 2003; Gadgil et al., 2000; Olsson et al., 2004). Adaptive co-management emphasizes learning-by-doing in management, where management objectives are treated as ‘experiments’ from which people can learn by testing and evaluating different management policies (Walters, 1986).

To date, a number of environmental organizations and neighborhood associations are demanding a voice in zoning and planning decisions that affect their communities (McDaniel and Alley, 2005). However, few approaches exist for their inclusion in biodiversity management activities. Hence, urban planners and decision-makers could use ELC-structures to serve as arenas for adaptive co-management in order to promote Local Agenda 21, and also to raise local environmental knowledge that often is low among urban residents (McKinney, 2002; Theodori et al., 1998).

5. Conclusions

Conservation biology increasingly needs to address the habitats in which human beings live, work, and play (Rosenzweig,

2003). Nowhere is this more pressing than in city-regions where scarcity of available natural land is high and where urban development generates some of the greatest species’ extinction rates on Earth. Novel approaches for biodiversity conservation and management should therefore be developed and tested in cities that also seek to incorporate urban residents and interest groups in biodiversity management activities. The Millennium Ecosystem Assessment recently pointed out the importance of developing incentives that promote multipurpose use of land and that stimulate cooperation among people and different sectors in society to support biodiversity (MA, 2005).

The review and synthesis of this paper suggests that ecological land-use complementation could become a useful urban planning approach for promoting biodiversity conservation in urban areas and for the incorporation of a larger segment of urban residents in biodiversity management. ELC is particularly useful to adopt in situations where efficiency in the use of available land needs to be well thought-out since it promotes biodiversity conservation without compromising the space used for other human activities (e.g., for human habitation and recreation). As indicated in this article, ecological land-use complementation could be used to support vital ecological processes in the design of new urban areas and to build resilience in urban ecosystems. The ecological premises behind this approach are supported by research on urban ecosystems, suggesting that the approach could be downscaled to local levels. The precise details of ELC need, however, to be worked out on a case-by-case basis depending on management goals and local social and ecological prerequisites. It requires collaboration among urban designers, landscape architects, ecologists, different interest groups, and private landholders, and as suggested herein, could be achieved by way of adaptive co-management. Potential ELC-structures in urban landscapes could be identified by way of GIS and serve as platforms for adaptive co-management for improving environmental conditions in the urban landscape. While more research on ELC is warranted in the years to come, the following guiding principles serve as useful rules of thumb for urban planning and design at local levels:

- (1) In the planning and design of new urban areas (especially suburbs), strive for the clustering together of different types of urban green patches to increase available habitats for species, to promote landscape complementation/supplementation functions, and to nurture key ecosystem processes essential for the support of biodiversity.
- (2) Plan so that potential ‘emergent’ ecological functions of a land use are realized, and so that ‘response diversity’ for different functional groups (i.e., pollinators, seed dispersers, pest-regulators) is accounted for in land-use designation.
- (3) Consider ways in which publicly and privately managed lands could support each other. Such considerations include ways to plan land development so to better take advantage of a diversity of management regimes to buffer against various natural disturbance (e.g., drought, fire) and socio-economic perturbations (e.g., economic cutbacks in management).
- (4) Adopt land-use complementation as specific ‘conservation targets’ to promote essential ecosystem services in city areas

where these might be especially critical to support, e.g., production landscapes.

- (5) Consider land-use complementation as an alternative to the designation of smaller and often quite inefficient protected areas in urban settings.
- (6) Identify and make use of existing ELC-structures in the landscape for the development of ‘arenas’ for experimental design and adaptive co-management. The goal of such sites could be the working out of adaptive management policies that will best meet the various needs of critical species (e.g., focal species), as well as promoting Local Agenda 21 in city-regions.

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References

- Altieri, M., Nelso Companioni, A., Cañizares, K., Murphy, C., Rosset, P., Bourque, M., Nicholls, C.I., 1999. The greening of the “barrios”: urban agriculture for food security in Cuba. *Agric. Human Values* 16, 131–140.
- Baines, C., 2000. How to Make a Wildlife Garden. Francis Lincoln Ltd., London.
- Bani, L., Baietto, M., Bottoni, L., Massa, R., 2002. The use of focal species in designing a habitat network for a lowland area of Lombardy, Italy. *Conserv. Biol.* 16, 826–831.
- Barker, G.M.A., 1997. A Framework for the Future: Green Networks With Multiple Uses in and Around Towns and Cities. English Nature, Peterborough, UK.
- Bennett, G., 2004. Integrating Biodiversity Conservation and Sustainable Use. Lessons Learned from Ecological Networks. IUCN, Gland, Switzerland, and Cambridge, UK.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188.
- Berkes, F., Colding, J., Folke, C., 2003. *Navigating Social–Ecological Systems: Building Resilience for Complexity and Change*. Cambridge University Press, Cambridge (United Kingdom).
- Bevington, A., 1991. Habitat selection in the dunnock *Prunella modularis* in northern England. *Bird Study* 38, 87–91.
- Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6, 506–519.
- Blair, R.B., 2001. Birds and butterflies along urban gradients in two ecoregions of the U.S. In: Lockwood, J.L., McKinney, M.L. (Eds.), *Biotic Homogenization*. Kluwer, Norwell, MA.
- Brennan, A.-M., 1992. The management of golf courses as potential nature reserves. *Asp. Appl. Biol.* 29, 241–248.
- Calkins, M., 2005. Strategy use and challenges of ecological design in landscape architecture. *Landscape Urban Plann.* 73, 29–48.
- Cane, J.H., 2001. Habitat fragmentation and native bees: a premature verdict? *Conserv. Ecol.* 5 (1), 3, <http://www.consecol.org/vol5/iss1/art3>.
- Cannon, A.R., Chamberlain, D.E., Toms, M.P., Hatchwell, B.J., Gaston, K.J., 2005. Trends in the use of private gardens by wild birds in Great Britain 1995–2002. *J. Appl. Ecol.* 45, 659–671.
- Carpenter, S.R., Folke, C., 2006. Ecology for transformation. *Trends Ecol. Evol.* 21, 309–315.
- Chamberlain, D.E., Cannon, A.R., Toms, M.P., 2004. Associations of garden birds with gradients in garden habitat and local habitat. *Ecography* 27, 589–600.
- Clergeau, P., Jokimäki, J., Savard, J.-P.L., 2001. Are urban bird communities influenced by the bird diversity of adjacent landscapes? *J. Appl. Ecol.* 38, 1122–1134.
- Colding, J., Lundberg, J., Folke, C., 2006. Incorporating green-area user groups in urban ecosystem management. *AMBIO* 35, 237–244.
- Cohen, S.Z., Nickerson, S., Maxey, R., Dupuy, A., Senita, J.A., 1990. A ground-water monitoring study for pesticides and nitrate associated with golf courses on Cape Cod. *Ground Water Monit. Rev. Winter*, 160–173.
- Cornelis, J., Hermy, M., 2004. Biodiversity relationships in urban and suburban parks in Flanders. *Landscape Urban Plann.* 69, 385–401.
- Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.T., Huntly, N., Naiman, N.J., Riebsame, W.E., Turner, M.G., Valone, T.J., 2000. Ecological principles and guidelines for managing the use of land. *Ecol. Appl.* 10, 639–670.
- Dair, I., Schofield, J.M., 1990. Nature conservation and the management of golf courses in Great Britain. In: Cochran, A.J. (Ed.), *Science and Golf*. Spon, London, pp. 330–335.
- Dawe, G.F.M., 1995. Species-density in relation to urban open space. *Land Contam. Reclamation* 3, 114–116.
- Dickman, C.R., 1987. Habitat fragmentation and vertebrate species richness in an urban environment. *J. Appl. Ecol.* 24, 337–351.
- Drayton, B., Primack, R.B., 1996. Plant species lost in an isolated conservation area in Metropolitan Boston from 1894 to 1993. *Conserv. Biol.* 10, 30–39.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 1, 488–494.
- Elmqvist, T., Alfsen, C., Colding, J. Urban systems. In: Jorgensen, S.E. (Ed.), *Encyclopedia of Ecology*. Elsevier, Oxford, UK, in press.
- Eybert, M.C., Constant, P., Lefevre, J.C., 1995. Effects of changes in agricultural landscape on a breeding population of Linnets *Acanthis cannabina* L. living in adjacent heathland. *Biol. Conserv.* 74, 195–202.
- Felson, A.J., Pickett, S.T.A., 2005. Designed experiments: new approaches to studying urban ecosystems. *Front. Ecol. Environ.* 10, 549–556.
- Fernández-Juricic, E., 2001. Density dependent habitat selection of corridors in a fragmented landscape. *Ibis* 143, 278–287.
- Fernández-Juricic, E., Jokimäki, J., 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodivers. Conserv.* 10, 2023–2043.
- Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Front. Ecol. Environ.* 4, 80–86.
- Flores, A., Pickett, S.T.A., Zipperer, W.C., Pouyat, R.V., Pirani, R., 1998. Adopting a modern ecological view of the metropolitan landscape: the case of a greenspace system for the New York City region. *Landscape Urban Plann.* 39, 295–308.
- Folke, C. Resilience: the emergence of a perspective for social–ecological systems analyses. *Global Environ. Change*, in press.
- Folke, C., Colding, J., Berkes, F., 2003. Synthesis: building resilience and adaptive capacity in social–ecological systems. In: Folke, C., Berkes, F., Colding, J. (Eds.), *Navigating Social–Ecological Systems: Building Resilience for Complexity and Change*. Cambridge University Press, Cambridge (UK), pp. 352–388.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* 35, 557–581.
- Foresman, T.W., Pickett, S.T.A., Zipperer, W.C., 1997. Methods for spatial and temporal land use and land cover assessment for urban ecosystems and application in the greater Baltimore–Chesapeake region. *Urban Ecosyst.* 1, 201–216.
- Fuller, R.J., 2000. Relationships between recent changes in lowland British agriculture and farmland bird populations: an overview. In: Aebischer, N.J.,

- Evans, A.D., Grice, P.V., Vockery, J.A. (Eds.), *Ecology and Conservation of Lowland Birds*. BOU, Tring, pp. 5–16.
- Fuller, R.J., Hinsley, S.A., Swetnam, R.D., 2004. The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. *Ibis* 146, 22–31.
- Gadgil, M., Seshagiri Rao, P.R., Utkarsh, G., Pramod, P., Chatre, A., 2000. New meanings for old knowledge: the people's biodiversity registers programme. *Ecol. Appl.* 10, 1307–1317.
- Gange, A.C., 1999. Dynamics of heathland conservation on a golf course. In: Farrally, M.R., Cochran, A.J. (Eds.), *Science and Golf III. Proceedings of the 1998 World Scientific Congress of Golf*. Human Kinetics, Leeds, UK, pp. 704–709.
- Gaston, K., Thompson, K., 2002. Gardens: heaven or hell for wildlife? Evidence for significance. In: *Biodiversity Conference Proceedings*, Royal Horticultural Society Conference Centre, Greycoat Street, London. In association with The Wildlife Trusts, www.rhs.org.uk/research/biodiversity (December 20, 2004).
- Greater London Authority, 2001. *Scrutiny of Green Spaces in London*. Greater London Authority, Green Spaces Investigative Committee, Romney House, London, http://mayor.london.gov.uk/assembly/reports/environment/green_spaces.rtf.
- Green, B.H., Marshall, I.C., 1987. An assessment of the role of golf courses in Kent, England, in protecting wildlife and landscape. *Landsc. Urban Plann.* 14, 143–154.
- Guerry, A.D., Hunter, M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conserv. Biol.* 16, 745–754.
- Gwyn, I., 2002. Gardens: heaven or hell for wildlife? Wildlife enhancement at Plas Tan y Bwch Gardens. In: *Biodiversity Conference Proceedings*, Royal Horticultural Society Conference Centre, Greycoat Street, London. In association with The Wildlife Trusts, <http://www.rhs.org.uk/research/biodiversity>, 2004-02-19.
- Hansen, A.J., Defries, R., Turner, W., 2004. Land use change and biodiversity: a synthesis of rates and consequences during the period of satellite imagery. In: Gutman, G., Justice, C. (Eds.), *Land Change Science: Observing, Monitoring, and Understanding Trajectories of Change on the Earth's Surface*. Springer Verlag, New York, NY, pp. 277–299.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.* 42, 3–16.
- Hardy, P.B., Dennis, R.L.H., 1999. The impact of urban development on butterflies within a city region. *Biodivers. Conserv.* 8, 1261–1279.
- Hinsley, S.A., Bellamy, P.E., Newton, I., Sparks, T.H., 1995. Habitat and landscape factors influencing the presence of individual bird species in woodland fragments. *J. Avian Biol.* 26, 94–104.
- Hobbs, R.J., 1993. Can revegetation assist in the conservation of biodiversity in agricultural areas? *Pac. Conserv. Biol.* 1, 29–38.
- Hobbs, R., 1997. Future landscapes and the future of landscape ecology. *Landsc. Urban Plann.* 37, 1–9.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hooper, D.U., Solan, M., Symstad, A., Diaz, S., Gessner, M.O., Buchmann, N., Delgrange, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E., van Peer, L., 2002. Species diversity, functional diversity, and ecosystem functioning. In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press Inc., New York, pp. 195–220.
- Hougnier, C., Colding, J., Söderqvist, T., 2006. Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden. *Ecol. Econ.* 59, 364–374.
- Kendle, T., Forbes, S., 1997. *Urban Nature Conservation*. E & FN Spon., London.
- Kühn, I., Brandl, R., Klotz, S., 2004. The flora of German cities is naturally species rich. *Evol. Ecol. Res.* 6, 749–764.
- Kulkarni, M., Dighe, S., Sawant, A., Oswal, P., Sahasrabudhe, K., Patwardhan, A., 2001. Institutions: biodiversity hotspots in urban areas. In: Ganeshaiha, K.N., Uma Shanker, R., Bawa, K.S. (Eds.), *Tropical Ecosystems: Structure, Diversity and Human Welfare*. Oxford/IBH, New Delhi/Calcutta, pp. 693–695.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* 7, 1109–1119.
- Lundberg, J., Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6, 87–98.
- MA (Millennium Ecosystem Assessment), 2005. *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, DC.
- Mason, C.F., 2000. Thrushes now largely restricted to the built environment in eastern England. *Divers. Distrib.* 6, 189–194.
- Maurer, U., Peschel, S., Schmitz, S., 2000. The flora of selected urban land-use types in Berlin and Potsdam with regard to nature conservation in cities. *Landsc. Urban Plann.* 46, 209–215.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McDaniel, J., Alley, K.D., 2005. Connecting local environmental knowledge and land use practices: a human ecosystem approach to urbanization in West Georgia. *Urban Ecosyst.* 8, 23–38.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. *Biol. Sci.* 52, 883–890.
- McNeely, J.A., Miller, K.R., Reid, W., Mittermeier, R., Werner, T.B., 1990. *Conserving the World's Biological Diversity*. IUCN/WRI/CI/WWF-US/World Bank, Gland, Switzerland.
- Melles, S., Glenn, S., Martin, K., 2003. Urban bird diversity and landscape complexity: species–environment associations along a multiscale habitat gradient. *Conserv. Ecol.* 7 (1), 5, <http://www.consecol.org/vol7/iss1/art5>.
- Morimoto, T., Katoh, K., Yamaura, Y., Watanabe, S., 2006. Can surrounding land cover influence the avifauna in urban/suburban woodlands in Japan? *Landsc. Urban Plann.* 75, 143–154.
- Naylor, R.L., Ehrlich, P.R., 1997. Natural pest control services and agriculture. In: Daily, G. (Ed.), *Nature's Services*. Island Press, Washington, DC, pp. 151–174.
- Oldfield, T.E.E., Smith, R.J., Harrop, S.R., Leader-Williams, N., 2003. Field sports and conservation in the United Kingdom. *Nature* 423, 531–533.
- Olsson, P., Folke, C., Hahn, T., 2004. Social–ecological transformation for ecosystem management: the development of adaptive co-management of a wetland landscape in Southern Sweden. *Ecol. Soc.* 9, 2, <http://www.ecologyandsociety.org/vol9/iss4/art2>.
- Pope, S.E., Fahrig, L., Merriam, H.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81, 2498–2508.
- Primack, R.B., 1993. *Essentials of Conservation Biology*. Sinauer Associates Inc., Sunderland, MA.
- Quin, A., Aviron, S., Dover, J., Burel, F., 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. *Agric. Ecosyst. Environ.* 103, 473–479.
- Ricketts, T., Imhoff, M., 2003. Biodiversity, urban areas, and agriculture: locating priority ecoregions for conservation. *Conserv. Ecol.* 8, 1, <http://consecol.org/vol8/iss2/art1>.
- Rodewald, A.D., Yahner, R.H., 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82, 3493–3504.
- Rosenzweig, M.L., 2003. *Win–Win Ecology: How the Earth's Species Can Survive in the Midst of Human Enterprise*. Oxford University Press, Oxford, UK.
- Savard, J.-P.L., Clergeau, P., Mennechez, G., 2000. Biodiversity concepts and urban ecosystems. *Landsc. Urban Plann.* 48, 131–142.
- Sandström, U.G., Angelstam, P., Khakee, A., 2006. Urban comprehensive planning—identifying barriers for the maintenance of functional habitat networks. *Landsc. Urban Plann.* 75, 43–57.
- Sala, O.E., Chapin, F.S.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Shapiro, A.M., 2002. The Californian urban butterfly fauna is dependent on alien plants. *Divers. Distrib.* 8, 31–40.

- Simberloff, D., 1986. Are we on the verge of a mass extinction in tropical rain forests? In: Elliott, D.K. (Ed.), *Dynamics of Extinction*. John Wiley, New York, pp. 165–180.
- Simberloff, D., Cox, J., 1987. Consequences and costs of conservation corridors. *Conserv. Biol.* 1, 63–71.
- Summers-Smith, J.D., 1999. Current status of the house sparrow in Britain. *Br. Wildl.* 10, 381–386.
- Szacki, J., Glowacka, I., Liro, A., Matuszkiewicz, A., 1994. The role of connectivity in the urban landscape: some results of research. *Memorabilia Zool.* 49, 49–56.
- Tanner, R.A., Gange, A.C., 2005. Effects of golf courses on local biodiversity. *Landscape Urban Planning* 71, 137–146.
- Terman, M.R., 1997. Natural links: naturalistic golf courses as wildlife habitat. *Landscape Urban Planning* 38, 183–197.
- Theobald, D.M., Hobbs, N.T., Bearly, T., Zack, J.A., Shenk, T., Riessame, W.E., 2000. Incorporating biological information in local land-use decision making: designing a system for conservation planning. *Landscape Ecol.* 15, 35–45.
- Theodori, G.L., Luloff, A.E., Willits, F.K., 1998. The association of outdoor recreation and environmental concern: reexamining the Dunlap-Heffernan thesis. *Rural Sociol.* 63, 94–108.
- Thompson, K., Austin, K.C., Smith, R.M., Warren, P.H., Angold, P.G., Gaston, K.J., 2003. Urban domestic gardens (I): putting small-scale plant diversity in context. *J. Veg. Sci.* 14, 71–78.
- Vandermeer, J., Carvajal, R., 2001. Metapopulation dynamics and the quality of the matrix. *Am. Nat.* 158, 211–220.
- Villard, M.-A., Trzcinski, K.M., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.* 13, 774–783.
- von Haaren, C., Reich, M., 2006. The German way to greenways and habitat networks. *Landscape Urban Planning* 76, 7–22.
- Walters, C.J., 1986. *Adaptive Management of Renewable Resources*. MacMillan, New York.
- Wiens, J.A., 1997. Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis* 137, S97–S104.
- Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2003. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biol. Conserv.* 115, 329–341.
- Wood, B.C., Pullin, A.S., 2002. Persistence of species in a fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. *Biodivers. Conserv.* 11, 1451–1468.
- Yasuda, M., Koike, F., 2006. Do golf courses provide a refuge for flora and fauna in Japanese urban landscapes? *Landscape Urban Planning* 75, 58–68.
- Young, C.H., Jarvis, P.J., 2001. Measuring urban habitat fragmentation: an example from the Black Country, UK. *Landscape Ecol.* 16, 643–658.