Biodiversity in golf courses and its contribution to the diversity of open green spaces in an urban setting

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Academic Dissertation

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Golf is a game whose aim is to hit a very small ball into an even smaller hole, with weapons singularly ill-designed for the purpose.
 - *Winston Churchill*

Contents

This thesis is based on the following articles:

I Saarikivi, J., Idström, L., Venn, S., Niemelä, J. & Kotze, D.J. 2010. Carabid beetle assemblages associated with urban golf courses in the greater Helsinki area. European Journal of Entomology 107: 553-561.

II Saarikivi, J., Knopp, T., Granroth, A. & Merilä, J. 2013. The role of golf courses in maintaining genetic connectivity between common frog (*Rana temporaria*) populations in an urban setting. Conservation Genetics 14: 1057-1064.

III Saarikivi, J. & Herczeg, G. 2014. Do hole-nesting passerine birds fare well at artificial suburban forest edges? Annales Zoologi Fennici 51: 488-494.

IV Saarikivi, J., Tähtinen, S., Malmberg, S. & Kotze, D.J. 2015. Converting land into golf courses – effects on ground beetles (Coleoptera, Carabidae). Insect Conservation and Diversity 8: 247-251.

Table of contributions:

	I	II	III	IV
Original idea	JS,JK,JN	JS,TK,JM	JS,HP	JS,JK
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Analysis	JS,JK	AG,TK	JS,GH	JS,JK
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Abstract

Ecologically simplified urban landscapes are often claimed to be useless nature with hardly any wildlife. Golf courses in particular are often claimed to be a poor use of land, ecologically speaking. They cover large areas, have a restricted entrance, are heavily managed and require a lot of resources in their up-keeping. These "green deserts" and "elitist people practicing their sport" have been subject to much debate and environmental concern. Populist, active and loud lobbying against the building of golf courses has created a popular opposition, although there is little scientific evidence to support their claims. Therefore, it is of interest to determine to what extent these claims are justified.

In this thesis, the ecological value of golf courses was assessed to determine how golf courses contribute to the diversity of open green spaces in an urban setting, by studying the biodiversity of established and newly-created golf courses in the greater Helsinki region, southern Finland. In a series of field experiments, the biodiversity of various animal groups (insects, birds, frogs) with distinct life histories was measured at urban or semi-urban golf courses. Each animal group was used to study different aspects of diversity. Species diversity and assemblages were studied using carabid beetles (articles I, IV), genetic diversity using the common frog (*Rana temporaria*) (II) and a case study to measure the quality of the golf course environment as habitat was performed using three hole-nesting bird species (great tit, blue tit and pied flycatcher), evaluating their nesting and reproductive success at golf course forest edges (III). Furthermore, the effects of constructing a golf course on carabid beetles were evaluated before (I) and after (IV) course development.

Golf courses appeared to be rich in carabid beetle species, very few of them rare or of conservation concern though. Beetle assemblages differed considerably between the golf courses studied and between the habitat types sampled on these courses, but not between course development stages (established vs. newly created vs. reference area). Genetic variation of common frog populations in golf courses showed little differentiation, suggesting that golf courses contribute positively to urban amphibian populations by providing suitable water bodies for reproduction and green corridors for dispersal, thus preventing isolation and loss of genetic variability within populations. Hole-nesting passerine birds showed a clear preference for golf course forest edges over the nearby forests. Birds also performed better in terms of nest occupancy and number of offspring at golf course forest edges, thus indicating a valuable habitat, which could be further improved with the addition of nest boxes.

The studies show that golf courses host high biodiversity and have conservation potential in ecologically simplified urban landscapes. Urban fauna seems resilient and capable of adapting to these highly modified environments, thus providing possibilities to enhance biodiversity though the combined and well-planned efforts of various practitioners.

Tiivistelmä

Kaupunkiluonnon väitetään usein olevan köyhää ja hyödytöntä luontoa, jossa tuskin mikään eliölaji viihtyy. Maankäyttö golfkenttiä varten on myös usein kyseenalaistettu samasta syystä. Golfkentät vievät paljon maapinta-alaa, niihin on rajoitettu pääsy ja niiden ylläpito vaatii runsaasti resursseja. Urheilulajina golfilla on ollut elitistinen leima ja se on saanut potea huonoa omaatuntoa ympäristöarvojen polkemisesta. Golfkenttiä on vastustettu milloin mistäkin syystä, usein vailla kovin vakuuttavia perusteita - ainakaan sellaisia, jotka liittyisivät luontoarvoihin. Golfkenttien luontoarvot on kyseenalaistettu mm. siksi, että tutkittua tietoa niistä on ollut todella vähän. Onkin paikallaan kysyä, millaisia luontoarvoja golfkentillä on tai voisi olla ja lähestyä aihetta tieteellisesti.

Tämän tutkimuksen tarkoituksena on tutkia golfkenttien luontoarvoja. Mielenkiinnon kohteena on urbaanien golfkenttien luonnon monimuotoisuus ja sen suhde ja merkitys kaupunkialueen luonnon monimuotoisuuteen. Tätä tutkitaan vertaamalla golfkenttien biodiversiteettiä ympäröivän luonnon biodiversiteettiin sekä vertaamalla kenttäalueiden biodiversiteettiä ennen kentän rakentamista ja sen jälkeen. Tutkimuseläiminä ovat hyönteiset, sammakot ja linnut. Eri eliöryhmien avulla päästään käsiksi biodiversiteetin eri tasoihin. Lajimonimuotoisuutta tutkitaan kovakuoriaisilla, maakiitäjäisillä (artikkelit 1 ja 4) ja geneettistä monimuotoisuutta sammakoilla (artikkeli 2). Golfkenttäympäristön laatua ja sen aktiivista parantamista lisääntymisympäristönä tutkitaan linnuilla (artikkeli 3), joiden lisääntymismenestystä arvioidaan kenttäympäristön linnunpöntöissä. Golfkenttien laajennuksen vaikutuksia maakiitäjäisyhteisöjen rakenteeseen onnistuttiin tutkimaan tekemällä mittauksia ennen (artikkeli 1) golfkentän laajennusta ja sen jälkeen (artikkeli 4).

Golfkentät osoittautuivat monimuotoisiksi ympäristöiksi. Maakiitäjäislajeja ja –yksilöitä on kentillä runsaasti, joskaan joukossa ei ollut harvinaisia tai uhanalaisia lajeja. Maakiitäjäisten lajiyhteisöt vaihtelevat huomattavasti kenttien ja eri elinympäristötyyppien välillä, mutta eivät juurikaan eroa kenttien, niiden laajennusalueiden tai niitä ympäröivien alueiden välillä. Golfkenttien sammakoiden geneettinen variaatio osoittautui vähäiseksi sekä kenttien sisällä että niiden välillä. Golfkentät eivät siis ilmeisesti rajoita sammakoiden geenivaihtoa, vaan saattavat toimia viheryhteyksinä lisääntymispaikkojen välillä. Pöntöissä pesivät linnut suosivat golfkenttien reunoilla olevia pönttöjä verrattuna läheisten metsien pönttöihin. Myös lintujen pesintämenestys golfkenttien reunoissa vaikuttaisi olevan parempi kuin lähiympäristössä.

Tutkimukset osoittavat että golfkentät kaupunkiympäristössä ovat monimuotoisia ja arvokkaita elinympäristöjä. Kaupunkiympäristön lajit pystyvät hyvin hyödyntämään golfkenttien elinympäristöä, jonka laatua voi entisestään parantaa aktiivisilla suojelu- ja luonnonhoitotoimilla.

1. Introduction

Urbanized areas cover about 4% of the Earth's surface, yet support more than half of the human population (Mock 2000, Niemelä 2011). These human-dominated environments have changed global ecosystems considerably (Vitousek et al. 1997). Urbanization not only causes habitat loss and fragmentation for the flora and fauna (McKinney 2006), but also increases the levels of air, soil and wetland pollution (Hamer & McDonnell 2008). This makes urbanization, together with climate change, one of the biggest threats to biodiversity and ecosystem functioning (McKinney 2002). But not all impacts of urbanization should be perceived as negative (Niemelä 2011). The variety of human impacts in urban areas diversifies the urban environment by modifying existing ecosystems and by creating unique ones (Gilbert 1989). Urban biodiversity is a result of the characteristics of urban habitats, such as highly fragmented habitat patches, mosaics with patches of harsh and inhospitable habitats, frequent disturbance events, early successional stages, high levels of nutrients, pollution and altered climatic conditions (Gilbert 1989, Niemelä 1999, Niemelä 2011). Consequently, biodiversity in cities may be higher than in more natural environments (Pickett et al. 2008).

Urban land-uses are particularly diverse, small-scaled and intensive (Niemelä 2011). The diversity of human activities in cities creates and maintains a variety of habitats ranging from fairly natural to highly modified, some of which do not occur elsewhere (Niemelä 1999). Natural systems tend to persist in the urban setting where strong geological features (i.e., rivers and geological contours) and land unsuitable for building exist. Guiding the construction and development of the city are also important factors, given that the density of buildings and infrastructure leaves either more or less room for nature. In certain cities, zoning regulations call for plenty of open spaces, which are usually developed as green spaces (Clark & Hietala 2006). Extensive modifications and management of natural habitats take place in urban parks, cemeteries, allotment gardens and sports sites. Varied attitudes and views about open spaces have shaped the city's recreational areas with leisure activities, such as sport, having a big impact on the creation and use of green spaces (Clark & Hietala 2006).

Nowadays, most people's experience of nature is urban. Recreational areas are essential for residents and their presence in the neighbourhood is an appreciated characteristic reflected in property prices (Do & Grudnitski 1995, Tyrväinen 1997). In addition to being important for residents, urban green areas also have intrinsic ecological value (Niemelä 1999), however previously largely ignored by ecologists (Pearce 1993). Preserving, conserving and enhancing the ecological value of habitats retained on private land and in public open-space areas requires a flexible approach that takes advantage of all opportunities to retain habitat and combining conservation efforts both in formal habitat reserves and in off-reserve habitats (Franklin 1993, Hodgkison et al. 2006). To identify potentially ecologically valuable urban green space habitats, sites that occupy large areas of land would be ideal, such as sports sites like golf courses. Few leisure activities have such an intimate interaction with the environment as golf (Tanner and Gange 2005). The expansion in the number of golf courses during recent decades has seen increasing concern over their role in the management of land and the impact they have on biodiversity (Hammond & Hudson 2007).

1.1. Golf courses

Worldwide, there are about 35 000 golf courses (Saito 2010) roughly equal to the number of McDonald's restaurants (ca. 34 000, McDonald's Corporation, 2013). New courses are being built at a rate that makes golf course development one of the fastest growing types of land development in the world (Terman 1997) with a strong correlation with economic growth (Colding & Folke 2009). This is not happening without environmental impacts and golf's effect on the environment is a hotly debated topic in many countries (Dodson 2000). In fact, golf is a sport that has been placed in the environmental spotlight, because it occupies such large areas of land, often close to urban centres where human welfare, wildlife health, water quality and other issues are of paramount importance (Stangel & Distler 2002) and land is expensive and scarce for any purpose. A typical 18-hole golf course comprises 54 ha of land (Terman 1997) and up to 70 % of that area is considered rough or out-of-play areas, that has the potential for creating significant wildlife benefits (Tilly 2000).

The public perception of golf courses is overwhelmingly negative, but this perception depends on whether one is actively involved with the game. In a survey of 400 people in south-east England in 2002, 80 % of respondents who play golf answered that courses are good for the environment, while among non-players 36 % felt that golf courses are environmentally beneficial. Among players, the most common reason for courses being beneficial was that they preserve areas of natural habitat. However, among non-players, the most common reason for courses being detrimental was that they destroy areas of natural habitat. The survey also showed that there is much anti-golf feeling amongst the general public (Gange et al. 2003).

Golf courses have historically been seen as places of heavy pesticide and fertilizer use, however, there are few scientific studies on the ecology of golf courses (Yasuda & Koike 2006). Habitat modification (Terman 1997), chemical contamination (Murphy & Aucott 1998), water management (Cohen et.al. 1993) and urbanization around golf courses (Markwick 2000) are all concerns that have been expressed by those who claim that golf courses are a poor use, ecologically speaking, of land (Platt 1994). However, until recently, there has been little evidence to support the view that golf courses are good or bad for the environment at the landscape scale. The little information that exists suggest that golf courses are not significant sources of water pollution (Cohen et al. 1999) and may be equal to many natural habitats in terms of animal and plant diversity (Terman 1997, Gange & Lindsay 2002, Colding & Folke 2009). There are only a handful of studies that employ a strict scientific method to the study of wildlife on golf courses (Blair 1996, Green & Marshall 1987, Terman 1997, Terman 2000, Yasuda & Koike 2005, Colding & Folke 2009, Colding et al. 2009). All studies have shown that golf courses compare well in terms of wildlife abundance and diversity to that of adjacent areas of land. A feature of these studies (e.g. Blair 1996, Terman 1997) is that the diversity of taxa on golf courses has been compared with areas of pristine natural habitat. As shown by Gange & Lindsay (2002), a more realistic question to ask, in terms of landscape ecology, is how the biological diversity of a golf course compares with that of the habitat from which the course was constructed. Land targeted for golf development has been almost exclusively farmland (Gange & Lindsay 2002), so it would be fruitful to compare biodiversity of golf courses with that of agricultural land. Tanner and Gange (2005) concluded that golf courses of any age can enhance the local biodiversity of an area by providing a greater variety of habitats than intensively managed agricultural areas (Tanner & Gange 2005). Similarly, Colding and Folke (2009) found higher ecological values in golf courses when compared with agricultural areas, but also emphasised the biodiversity illusionary effect in which species replacement leads to an increase in biodiversity at the local scale at the expense of overall regional biodiversity.

Nowadays, several golf courses contribute to sustaining threatened flora and fauna regionally (Colding & Folke 2009). Furthermore, many golf courses actively promote nature conservation and harbour some of the rarest plant and animal species (Gange et al. 2003). Also, golf courses can participate in environmental management programmes and their efforts are being recognized through a national awards programme in the UK (Gange et.al. 2003), fostering a significant trend in golf course management to create more naturalistic landscapes (Santiago & Rodewald 2004). Also, there is much that can be done to golf courses to enhance the quality of habitats they possess and ecologists can help course managers to maximize the conservation potential of specific habitats. Since management is intensive at golf courses, it is possible that management regimes could be altered for the benefit of both the players and wildlife. Potentially, urban golf courses could become more purposefully designed and managed for biodiversity and the promotion of critical ecosystem services (Colding & Folke 2009).

Undisturbed, pristine habitats are commonly the choice of ecologists to understand nature. However, with the spread of urbanization, ecologists also need to study human-dominated landscapes such as golf courses or other urban green space areas. They are potentially a major ecological resource and provide a significant opportunity for increasing awareness regarding urban biodiversity. Furthermore, the link between ecosystem health and human health and well-being is known, although - due to its complexity - not yet fully understood (de Vries et al.2003, Tzoulas et al. 2007, Sandifer et al. 2015). Therefore, developing and enhancing so called green infrastructure in planning for the purpose of reducing health care expenditure, provides not only significant economic savings, but also improves environmental quality (Tzoulas et al. 2007, Tzoulas & Greening 2011).

A comprehensive understanding of the recreational land-use of golf is motivated by the number of golf courses, the large green area habitats they constitute and the potential the golfing sector has in sustaining biota and ecosystem processes on golf courses (Colding & Folke 2009). In this study, the ecology of golf courses is assessed by monitoring the biodiversity of various animal groups. When measuring diversity, a complete inventory of all species is impossible due to time and effort constraints. Therefore, we chose indicator groups that were relatively easy to observe and identify. The spatial scale of microhabitats within golf courses provided a relevant framework for studies with insects, in this case ground beetles (Carabidae), that are actively studied (by colleagues) in the region (e.g. Noreika & Kotze 2012, Kotze et al. 2012, Venn et al. 2013). Species responses to environmental variability and anthropogenic processes can be determined from the structure of the species community. Changes in species compositions could be monitored on a temporal scale from days to years. A far greater temporal scale was achieved with genetic studies done on frogs. Historical development of genetic diversity and differentiation reveals the degree of connectivity between populations. Behavioural responses to active measurements of habitat improvement were tested using birds. By adding resources, nest boxes, for small hole-nesting passerine birds, the quality of a golf course environment as a breeding habitat could be evaluated. Overall, the variety of taxa selected and methodological diversity allows for a better understanding of the ecology of golf courses.

1.1.1. Invertebrates on golf courses

Invertebrates have important functional roles as, e.g. herbivores, pollinators and as prey for a variety of birds (Samways 1997). Due to their small size, invertebrates also do not disrupt the smoothness and uniformity of a golf course or do not otherwise impact the game. However, some taxa like earthworms or ants can be a nuisance or pests in golf courses when they occur in large numbers and produce castings or mounds on low-cut turf like putting greens, approaches and collars, tee boxes and fairways. Occasionally, there are efforts in controlling them in golf courses (Lopéz et al. 2000, Maier & Potter 2003, Williamson & Hong 2004).

Ground beetles (Coleoptera, Carabidae) are one of the best-known taxa in entomology. The wealth of knowledge, gathered though generations of carabidologists, have clarified the taxonomy and phylogeny, geographic distribution, habitat associations and ecological requirements, life history strategies and adaptations, especially in Europe (Kotze et al. 2011). Ecological research questions can be tested with carabid beetles, thanks to their sensitivity to environmental changes. Species' responses to habitat variability and natural and anthropogenic processes may be determined by different factors such as species richness, abundance and assemblages (Kotze et al. 2011). The relative ease of collecting carabid beetles using pitfall traps (Greenslade 1964) makes long term data collecting possible and results comparative. Carabid beetles have also been used as indicator species in some studies in golf courses (Tanner & Gange 2005, Colding & Folke 2009).

Carabid beetle studies in urban areas have shown that diversity often peaks at moderately disturbed environments, such as ruderal habitats, domestic gardens, meadows and parks (Niemelä et al. 2002, Niemelä & Kotze 2009, Niemelä 2011, Venn et al. 2013). Tanner & Gange (2005) showed that carabid beetle species richness and abundance are higher in golf courses than in the agricultural land from which the golf course had been created. They attributed the difference in beetle numbers to courses having heterogeneous habitats, which provide varying microclimates. Insect communities in boreal landscapes are often more diverse in open areas than in forests, also land-use changes from monocultural fields to areas with small-scale habitat mosaics, such as golf courses with their fairways, bunkers, roughs, small forest patches and water bodies, tend to host high species richness (Colding & Folke, 2009).

1.1.2. Amphibians on golf courses

Increasing concerns regarding the disappearance of amphibian populations has captured global attention because of the well-documented declines at local, regional and even global scales (Stuart et al. 2004, Hamer & McDonnell 2008). A variety of factors have been implicated in these declines (e.g. introduced predators, fertilizers, pollutants and UV-B radiation in sunlight) and one of the leading factors is the impact of habitat fragmentation on pond-breeding amphibians (e.g. Blaustein & Wake 1990, Alford & Richards 1999, Lehtinen et al. 1999, Houlahan et al. 2000, Pahkala et al. 2002). Typically, amphibians decrease in richness with increasing urbanization due to direct loss of habitats and decreasing water quality, and the presence of predators (e.g. Rubbo & Kieseker 2005), but there are some studies that have indicated that amphibians may show high levels of species diversity in urban areas, in which also rare species could be found (Castro et al. 2003).

Impacts of golf course design and management on amphibian populations have received some research attention (e.g Howard et al. 2002, Paton & Egan 2002, Colding et al. 2009, Colding & Folke 2009). Golf course wetlands can support amphibian species that have lost valuable wetland habitats elsewhere in urban areas and if developed and maintained thoughtfully, they may have potential to function as mini-preserves for even some of the rarer or more sensitive species or species of conservation concern (Colding et al. 2009). Generally, amphibians seem to prefer ponds that dry annually (to avoid predation by fish), are not very sensitive to grass height around ponds, but are more likely to disperse through forested landscapes and often avoid moving across broad expanses of turf, such as fairways or greens (Paton & Egan 2002). Decreased fitness in amphibians at golf courses has even been demonstrated in colour pattern asymmetry as a correlate of habitat disturbance (Wright & Zamudio 2002). The casual observation that certain amphibian species are thriving in heavily treated environments can lead to erroneous conclusions regarding long term impacts. In order to maintain amphibians at golf courses, attention must be paid to the integrity of the whole ecosystem where ponds, movement corridors and habitats during the breeding and non-breeding seasons are considered. Seasonal wetlands are considered very effective in enhancing amphibian diversity in golf courses (Metts et al. 2002).

A number of studies have shown genetic effects of fragmentation at a fine scale within cities, where a combination of restricted gene flow, founder effects and small effective population size shape the genetic structure of urban populations (see Kotze et al. 2011). Amphibians with their limited dispersal ability may exhibit population genetic patterns consistent with loss of population connectivity. Barriers associated with urban habitats promoted genetic population differentiation, and despite the lack of any absolute barrier to movement between ponds, substantial genetic differentiations in urban amphibian populations have been found between sites separated by (on average) 2.3 km only (Hitchings & Beebee 1997).

1.1.3. Birds on golf courses

Birds are likely the most studied vertebrate group on golf courses. They are relatively easy to monitor and the ecology, behaviour and habitat needs of many species are well known. Many recent studies on wildlife of golf courses have focused on birds (e.g. Gillihan 2000, Gordon et al. 2003, Dale 2004, White & Main 2004, Merola-Zwartjes & DeLong 2005, Rodewald et al. 2005, Smith & Conway 2005, Cristol & Rodewald 2005, Cornell et al. 2011). These studies have shown that golf courses can provide suitable habitats for many bird species and in some cases can even support birds that are of conservation concern. Recently, golf courses have played an important role in the conservation efforts for species like the eastern bluebird (*Sialia sialis*), tree swallow (*Tachycineta bicolor*), purple martin (*Progne subis*), red-cockaded woodpecker (*Picoides borealis*) and osprey (*Pandion haliaetus*) (Tilly 2000, Cornell et al. 2011). This is not to suggest that golf courses can fill the ecological roles of natural landscapes or support biodiversity present in native ecosystems, but they may provide supplementary resources like specific habitat components to some declining habitat specialists (Cristol & Rodewald 2005).

In Northern America, populations of the previously common red-headed woodpecker (*Melanerpes erythrocephalus*) have declined because of the loss of its natural habitat (oak savanna, farmlands and other open habitats with trees), but the species has benefited from highly modified habitats of golf courses, where old, large trees suitable for nesting and open woodland still occur (Rodewald et al. 2005). Other declining open habitat species, like the burrowing owl (*Athene cunicularia*) has also benefited from open foraging areas, lower predation rates and even artificial burrows in golf courses in south-central Washington (Smith & Conway 2005).

But there are also species that avoid golf courses and species that are negatively affected by them. Long term monitoring of the endangered ortolan bunting (*Emberiza hortulana*) in Norway showed that the species does not find golf courses attractive. Although calling males were present at a golf course, the low pairing success (and other indicators) suggests that females avoided the golf course, indicating the unsuitability of the habitat for breeding and thus resulted in a less sustainable population (probably even a sink) (Dale 2004).

Golf courses can support a greater number of birds than surrounding natural areas (Merola-Zwartjes & DeLong 2005), a response that is common throughout studies of avian responses to urbanization (Emlen 1974, Hohtola 1978, Beissinger & Osborne 1982, Green 1984,). It should be noted, however, that although overall species richness and diversity may increase in golf courses, the original and native bird community may suffer negative consequences. The loss of bird diversity is likely when development occurs in an area that originally had a high diversity of habitats (Colding et al. 2009). Also, the high numbers of birds do not necessarily reflect high quality habitat and the large number of birds that are relatively widespread and abundant may even be considered pests or nuisance species (e.g. starlings, *Sturnus vulgaris*) (Merola-Zwartjes & DeLong 2005).

1.2. Aims of the thesis

The primary aim of this thesis was to determine how golf courses contribute to the biological diversity of open green spaces in an urban setting. This was achieved through the study of various animal groups (insects, birds, frogs) with distinct life histories that were used as indicators of biodiversity. Each animal group was used to study different aspects of diversity. Species diversity and assemblages were studied using carabid beetles (papers I & IV), genetic diversity with the common frog (*Rana temporaria*) (paper II) and a study was performed to measure the quality of the golf course environment as habitat for three hole-nesting bird species (great tit, blue tit and pied flycatcher), evaluating their nesting and reproductive success at golf course - forest edges (paper III). Furthermore, the effects of constructing a golf course on carabid beetles were evaluated before (I) and after (IV) course development. The objective of this study was to determine the potential of golf course habitats to enhance urban biodiversity.

2. Materials and methods

All studies were performed on golf courses in the greater Helsinki area, southern Finland (Table 1, Fig. 1). Of the 30+ golf courses in the region, nine were selected as study sites. These courses represent a range of ages, from old (Tali established in 1932, the oldest golf course in Finland) to relatively new courses (est. 1987-2001) and their expansion areas that were developed during the study period (2009-2013).

Table 1. The studied golf courses in the greater Helsinki region. See Fig. 1 for course localities.

Name	Year established	size (ha)	expansion in (year)	expansion size (ha)	distance to city centre (km)
Tali	1932	55			6
Master Golf	1987	80			22
Talma 1&2	1989	70&60			36
Luukki	1990	32			25
Gumböle	1991	28	2009	22	19
Paloheinä	1996	15	2011	15	10
Hiekkaharju	1999	17	2011	40	17
Vuosaari	2001	50			14

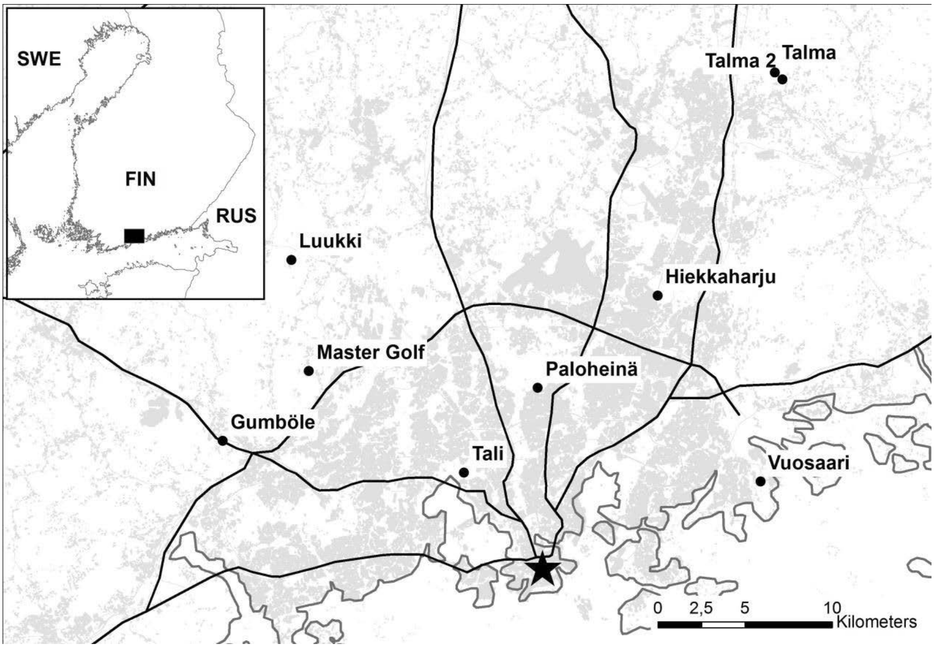

Figure 1. Map of golf courses in this study. Urbanized areas are in grey and the location of Helsinki city centre is marked by a star.

2.1. Pitfall trapping of carabids (papers I & IV)

Carabid beetles were collected using pitfall traps (Greenslade 1964). Traps were sunk into the ground with their openings flush with the soil surface. The placement of traps was similar in the two studies with traps placed in transects 5 m apart. The traps (diameter of opening 65 mm, volume 250 ml) were partly filled with a 70% aqueous propylene-glycol solution (30 ml per trap) to kill and preserve the trapped insects. Brown plastic lids, 100 cm^2 in size, were placed a few centimetres above the traps to prevent dilution by rainfall. The beetles were identified by JS and M.Sc. students Laura Idström (I), Saara Tähtinen (IV) and Sampsa Malmberg (IV). The nomenclature follows Lindroth (1985, 1986).

For the first study (I), 70 traps were set at each of the two full-sized courses (Tali and Vuosaari). At the three 9-hole courses, 35 traps were placed in the current course area and another 35 traps in the areas into which the courses were to be extended. The reason for sampling the areas into which the golf courses were to be extended was to monitor the changes that might occur in the carabid beetle assemblages once the areas are developed as golf courses. Continuous sampling started in early May, with traps emptied three times between then and late September 2007.

For the fourth study in 2011, we sampled the old and new (expansion area) course areas and nearby forest/field areas for reference. The traps, 72 per course, were placed in differently-managed habitat types at the golf courses and their expansion areas, including fairway edges, fields (roughs) and forest patches, that is, a representative spectrum of the vegetation types at these courses. At the nearby reference areas, the traps were set in forested and open habitat types, representing fields and forest patches of the course area. Since the most intensively managed habitat type sampled (fairway edge) cannot be found in nature, only forests and open habitats were sampled at reference areas.

2.2. Genetic study (paper II)

Common frog (*Rana temporaria*) tadpoles were genotyped with 13 polymorphic microsatellite markers. Frog eggs were collected from golf course ponds and nearby reference sites (ponds within 1 km from the golf course). The eggs were raised to tadpoles, anesthetized with MS-222 and stored in 70 % ethanol at +4° C. Since the common frog is a protected species in Finland, permission for sampling was granted from the local environmental authority (Suomen Ympäristökeskus, decision nr. LUO 213). Two frog eggs were collected from each spawn clump. One was used in the analyses and the other one served as a backup. Only relatively large and complete looking clutches were sampled to minimize the risk of sampling two clutches laid by the same female. DNA was extracted from nose tissue following Ivanova et al. (2006).

Golf courses were chosen on the basis of the presence of potentially suitable small water bodies as breeding habitat for frogs. Also, current land-use practices in the surroundings of these golf courses were similar to those in typical residential areas and recreational coniferous forest. From each golf course, one population was sampled, except from Talma golf, which due to its substantially larger size (130 ha; Table 1), two populations of *R. temporaria* was assumed to exist there. Within 1–2 km from the golf courses, six natural habitats with long-established breeding sites were sampled as reference sites, leading to a total of 12 sampled populations. Sampling was conducted at the spawning season in late April 2009.

2.3. Birds (paper III)

We tested the edge effect at golf courses through an experiment in which we placed wooden nest-boxes at the golf course – forest edge as well as 50 m into the forest. A line of 20 boxes was placed at the golf course forest edge and another line of 20 boxes, 50 m into the forest at five golf courses, making a total of 200 nest boxes. These boxes were 30 cm × 15 cm × 15 cm (height, width and depth) in size, with a hole diameter of 32 mm (+ plastic hole protectors / predator guards) (Clamens & Isenmann 1989). The nest-boxes were monitored weekly, with extra efforts during the incubation period in spring 2008. We recorded the species occupying nest-boxes and counted eggs and chicks. The nestlings were ringed before fledging. The type of nest boxes is suitable for species like the great tit, blue tit and pied flycatcher. These common species are affected negatively by the lack of nesting sites in urban forests (Marzluff & Ewing 2001).

2.4. Data analyses

The main statistical methods used to evaluate the carabid beetle assemblage structure were rank-abundance plots, diversity indices and rarefaction curves. Rank-abundance plots graphically depict the dominance and evenness structure of the beetle assemblages (Magurran 2004). Diversity and evenness indices reveal different aspects of the composition of the assemblages. Rarefaction curves reflect species richness that compensate for varying sample sizes. Comparisons of assemblages between the different golf courses were explored using non-metric multidimensional scaling (NMDS), while the responses of individual species to golf courses and their habitat types were evaluated using generalized linear mixed models (GLMM).

The carabid beetles were classified into broad morphological and ecological categories according to the literature (e.g. Lindroth 1985, 1986). Many species show clear preferences for certain habitats or particular site preferences. We used classifications based on habitat associations (forest, open habitat, generalist species) and moisture conditions (dry, moist). Similarly, the colonization abilities of carabid beetles were evaluated through their classification into macropterous (long-winged, flight capable), brachypterous (short-winged, not capable of flight) or dimorphic species. Since carabid beetles are actively studied in Finland, a national frequency points system is available that is used to indicate the scarcity of species. These points indicate the number of 10 km grid squares from which the species have been recorded during the period 1960–1990 in Finland (Rassi 1993).

A series of tests were performed for the genetic data. All loci were tested for the presence of null-alleles (van Oosterhout et al. 2006) and probabilities for Hardy–Weinberg equilibrium were tested for each locus (Raymond & Rousset 1995). Signs of recent shifts in population size were tested with the Wilcoxon test (Cornuet & Luikart 1997) and the substructuring of all populations was quantified by Weir and Cockerham's (1984) standardized F_{ST}, with a permutation test using Bonferroni correction to adjust the statistical significances of the F_{ST}. An analysis of isolation by distance based on the F_{ST} estimates was performed using the Mantels test (Mantel 1967) and the substructuring of the populations was further analysed with a Bayesian approach using the group level mixture analysis (Corander & Marttinen 2006).

The bird data were analyzed using a log-linear analysis followed with a generalized linear mixed model (GLMM) with Poisson distribution and log link. The computer programmes used in the analyses were PASW Statistics 18 (PASW Inc. Chicago, Illinois), SAS 9.2 (SAS institute Inc., Cary, NC, USA), Microchecker 2.2.3, FSTAT 2.9.3.2, GenePop 4.0.1.0, Bottleneck 1.2.02, BAPS 5.2 and the R statistical software (R Development Core Team 2011) in which vegan and lme4 libraries were used.

3. Results and Discussion

Golf courses in the Helsinki region hold promising ecological value in terms of biodiversity. A diverse fauna of carabid beetles was found, frogs showed unrestricted genetic variation compared to natural sites and birds performed well in terms of their reproductive output at golf course – forest edge sites.

3.1. Rich carabid fauna on golf courses

As the golf courses consisted mainly of open, grassy habitats, it was not surprising that they were dominated by open habitat or generalist carabid species. Nevertheless, it was surprising that such a large number of species was found in these golf course sites. Our catch of 71-72 species is considerably more than what has been caught in comparative habitats with similar effort in the region (Venn et al. 2003, Niemelä & Kotze 2009). Furthermore, having roughly the same number of species from these golf courses in separate studies indicated the high overall diversity, but also revealed that only 70% of the species were the same among golf courses. Our interpretation is that there is no particular golf course fauna of beetles, but instead, the courses are unique in terms of their carabid assemblages. They retained many elements from the pre-existing habitats and their fauna.

It also seemed that carabid beetles were quick to colonize novel environments, i.e. the expansion areas. Many species showed clear preferences for certain site characteristics. The assemblages of species in golf courses consisted mainly of common, widespread, generalist and open-habitat species, but even the tiny fragments of forest appeared adequate for some forest species to exist. It may be that it is not just "habitat as such" that is important for species, but certain structural elements they require: dead wood of certain types and amounts, certain host plant species, bare patches of grassy sand dunes, mudflat patches at wetland ponds, etc. Hence, if the aim is to improve conditions for species that require conservation efforts (which are currently not the studied carabids), one should create such structures in areas other than the fairways. This puts the role of habitat structure and habitat manipulation in perspective: course design and management practices can significantly influence the local carabid fauna.

As we showed in studying golf course construction, the courses (old and the newly created expansion areas) hosted a higher carabid beetle diversity compared to the reference areas. This is possibly due to the increased habitat diversity in golf courses. Open grasslands and meadow-like roughs create a warmer microhabitat and host a greater variety of vegetation than forests or agricultural land. Ponds, ditches and sand bunkers further add to the heterogeneity of the golf course environment. These diverse habitats, although small in size, provide resources for a diverse fauna of insects, such as carabids.

Our results on carabids support the notion that the positive relationship between habitat diversity and species diversity is one of the reasons why urban areas often show high diversity when compared to rural areas. Urban biodiversity is often further increased with a higher number of alien species. Namely, biodiversity often peaks in moderately disturbed habitats due to an increase in species that are anthropophilous (McKinney 2002, Colding & Folke 2009). However, it is important to keep in mind that diversity alone is not necessarily an adequate measure of the quality of nature. High diversity could be found in areas of high anthropogenic influence or diversity can be promoted through active measures such as the introduction of alien plants that attract new insect species with potentially harmful effects.

Urban green spaces, such as golf courses can sometimes be examples of the "biodiversity illusionary phenomenon (= BIP effect)" (Colding & Folke 2009) in which the local biodiversity can increase at the expense of overall biodiversity. Constructing a golf course into a native habitat fragment may increase the diversity at the course area, but at the same time increases the risk of losing disturbance-sensitive species, such as those that are interior-dependent. Our results on carabids provide some support for the theory, as the increase in biodiversity is achieved through an increase of common and generalist species. Yet, we found that beetle assemblages differed considerably between the three golf courses studied and between the habitat types sampled, but not between course development stages (established vs. newly created vs. reference area) (Paper IV). Whereas the BIP effect may be more evident with larger species, such as birds, we argue that the regional, city-wide, species pool of carabids consists of many resilient beetle species that are capable of rapidly colonizing golf course environments. At our urban or semi-urban golf course habitats the species pool may have been already purged of habitat specialist species due to urbanization pressures in the past (Balmford 1996, Hartley et al. 2007, Colding & Folke 2009).

3.2. Amphibians showed little genetic differentiation

Constructing a golf course often involves management of small water bodies in the course area. The quality of the turf or lawn is essential for the game. Water is needed for irrigation and excess water is lead to ditches. Ponds make challenging obstacles for the game, are esthetically pleasing and may provide resources and habitat for wildlife.

The lack of suitable breeding ponds is a limiting factor for the occurrence of amphibians in urban areas (Beebee 1979, Vizyova 1986, Van Buskirk 2005). The common frog (*Rana temporaria*), being the most abundant amphibian in our study region, is an example of a species that is constantly looking for suitable breeding sites. In order to avoid fish - the predators of tadpoles - it favours seasonal wetlands or ponds that dry annually. Our study showed that the most urban golf courses had the largest breeding colonies of frogs, although the number of ponds was comparable with rural sites. The golf course sites were established relatively recently, whereas natural sites have been known as frog breeding sites for decades. Results from other sites confirm that golf course ponds may develop into frog breeding sites in a couple of years (Ostergaard et al. 2008). It seems that the conditions in golf course ponds are favourable for frogs, but in semi-urban or rural regions there are also a number of similarly suitable ponds in the nearby natural areas. In the most urban areas, golf course ponds may be among the only available ponds in the region and consequently hold larger gatherings of breeding individuals.

Our results revealed that the genetic differentiation of common frogs in the study area was very low, thus indicating unrestricted gene flow between populations in the golf courses. Seemingly relatively isolated urban populations displayed the highest F_{ST} –values, which could be an indication for isolation induced by urbanization or golf course construction, but generally hardly any genetic differentiation or isolation by distance was found.

Our interpretation is that golf course environments provide both favourable breeding sites as well as green corridors for migration. Even though golf course landscapes, which mainly comprise open lawns, do not seem favourable for frogs, there may be some elements, such as ditches or meadows that can serve as green corridors to nearby surrounding environments. The breeding of common frogs in golf course ponds show that some species use these areas periodically. Another example is migratory birds that frequently visit golf courses on their routes. The ecological role of golf courses has sometimes been described as stepping stones or buffer zones between nature and urban infrastructure (Terman 1997).

3.3. Positive edge effects for birds

If golf courses support high species diversity or genetic diversity at the landscape level, it is of interest to know how successful the wildlife is at these golf courses. We tested this by manipulating the breeding conditions in the golf courses by adding nest boxes for hole-nesting passerine birds at the course edges as well as nearby forests. The results show that both nest occupancy and the number of offspring were significantly higher at the artificial edges than at 50 m into the original forests.

The positive edge effect was very strong in our study indicating that the habitat mix, characteristic of edges, is attractive to species that tend to be tolerant of disturbances at their nesting habitats (Dowd 1992). It is possible that the quality of the edge habitat overrides the risk of increased disturbance and predation.

A concept of an ecological trap (Dwernychuk & Boag 1972) is sometimes attributed to golf courses: animals choose to settle in low-quality habitats over the other available habitats of higher quality. Individuals are misled on environmental cues that help them to identify high-quality habitat and the attractiveness of the habitat does not correlate positively with the survival or reproductive success of individuals actually choosing it (Weldon & Haddad 2005). Our result of higher nest occupancy at the golf course sites does not allow us to reject the ecological trap idea, but since reproductive success (number of offspring per nest), was also higher at the edges than in the forest, we can reject the hypothesis that the studied golf course forest edges acted as ecological traps.

4. Conclusions

Researchers and biologists have shown that a great deal of biodiversity can be found in highly modified environments. Urban areas are often richer in species than their rural counterparts (Gilbert 1989, Niemelä 2011). Biodiversity often peaks at areas that may seem like poor quality nature: dumping sites, wastelands, cemeteries, parks, urban centers and even sports sites, such as golf courses. Anthropogenic influences contribute positively to biodiversity through providing resources for some native species and a number of alien species. Diversity often found in urban areas increases the value of urban habitats and the few remaining habitat patches within the urban matrix are often highly valuable not only for urban wildlife, but also for residents and other urban dwellers as recreational space (Clark & Hietala 2006, Niemelä 2011).

This work supports earlier findings of high diversity in urban areas (Gilbert 1989, Niemelä 2011). The assemblages of beetles are distinct and variable between the golf courses studied and beetles seem to be resilient to changes and are quick to adapt to novel environments. The lack of rare species might indicate some species replacement in which generalist species occupy the niches (such as small forest patches in golf courses) previously inhabited by specialists. Nevertheless, in the disturbed environments in golf courses, even tiny habitat patches might support the fauna characteristic for that habitat type. Therefore, small and fragmented urban habitats might be valuable for conservation, as long as key habitat characteristics are preserved. Environmentally conscious management plays an important role in retaining these values (Niemelä 2001).

The study also confirmed that active measures can promote biodiversity or improve conditions for the golf course fauna. Nest-box addition considerably increased the nesting success of some common bird species. Specifically targeted conservation measures could be easily fulfilled and if planned correctly, could benefit both nature and possibly also the economy through the marketing of environmentally friendly golf course management practices.

As the level of genetic variation of frogs in urban and sub-urban golf courses revealed hardly any differentiation, and since the golf course ponds turned out to be a valuable breeding environment for the species, we may conclude that small water bodies are a key element in golf courses with high ecological values and should be promoted. Unrestricted gene flow also indicates a habitat suitable for at least the species studied.

Biodiversity conservation should not entirely be centered on protected-area management. Urban green spaces are often species rich and valuable, if not from the perspective of conserving rare or endangered species, but from the fact that they are important recreation areas for residents. Relatively large and numerous sports grounds in urban areas are better alternatives than built infrastructure. In fact, constructing a sports area like a golf course is often a way to save at least a proportion of nature, when the only other available option is tarmac and buildings.

Sport disciplines have their lifespan. Recently, golf has shown a decrease in popularity in some areas, share prices have decreased in value in some courses and the construction of new courses is decreasing, possibly because of the economy (e.g. Anon. 2012). The courses, once built on poor quality land, have retained some elements of the pre-existing or nearby nature, with a dose of new or additive diversity as a result of environmental changes – the ones part of urban nature.

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