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ANALYSIS

Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden.

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Abstract

Most economic valuation studies of species derive from stated preferences methods. These methods fail to take into account biodiversity values that the general public is not (made) informed about or has no experience with. Hence, production function (PF) and replacement cost (RC) approaches to valuation may be preferable in situations where species perform key life support functions in ecosystems, such as seed dispersal, pollination, or pest regulation. We conduct an RC analysis of the seed dispersal service performed by the Eurasian Jay (Garrulus glandarius) in the Stockholm National Urban Park, Sweden. The park holds one of the largest populations of giant oaks in Europe, and the oak (Quercus robur and Q. petrea) represents a keystone species in the hemiboreal forests. The primary objective was to estimate the number of seed-dispersed oak trees that resulted from jays and to determine the costs of replacing this service though human means. Results show that depending upon seeding or planting technique chosen, the RC per pair of jays in the park is SEK 35,000 (USD 4,900) and SEK 160,000 (USD 22,500), respectively. Based on the park's aggregated oak forest-area, average RC for natural oak forest regeneration by jays is SEK 15,000 (USD

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2,100) to SEK 67,000 (USD 9,400) per hectare, respectively. These estimates help motivating investments in management strategies that secure critical breeding and foraging habitats of jays, including coniferous forests and jay movement corridors. The analysis also illustrates the need for detailed ecological-economic knowledge in a PF or RC analysis. The continuous temporal and spatial oak dispersal service provided by jays holds several benefits compared to a man-made replacement of this service. PF and RC approaches are particularly motivated in cases of known functional ecological relationships, and critically important in estimating management measures where mobile link organisms and keystone species form key mutual relationships that generate high biodiversity benefits. In relation to obtained results, we discuss insights for conducting valuation studies on particular species.

Keywords: Replacement cost valuation; Ecosystem services; Seed dispersal; Oak; Eurasian Jay

1. Introduction

Ecosystem services can be defined as ecosystem functions that support and protect human activities or affect human well-being (Barbier et al., 1994). Alternatively, they can be defined as "…the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life" (Daily, 1997:3). Such anthropocentrically defined services include, among others, the maintenance of the atmospheric composition, climate amelioration, flood controls, drinking water supply, waste assimilation, nutrient recycling, soil regeneration, crop pollination, food provisioning, maintenance of species and genetic diversity, the maintenance of the scenery of a landscape, recreational sites, and aesthetic and amenity values (Costanza and Folke, 1996).

A critical challenge in ecological research is to understand what sustains the capacity for the generation of these services (Folke et al., 2004). For example, for long-term sustenance of the flows of natural resources (e.g., seafood, forage, timber, biomass fuels, fibres, pharmaceuticals, and other ecosystem goods) it is key to understand the underlying processes and functions that contribute to and make such flows possible. For instance, nearly one-third of the US food supply by volume depends on animal pollinators (cf. Kremen et al., 2004). Hence, sustaining this productivity requires the sustenance of resources required by pollinators throughout their life-history cycles, such as conservation of critical habitats near agricultural fields (Kremen et al., 2004), or the sustenance of habitats of natural enemies for control of insect pests that may reduce crop productivity (Östman et al., 2003). Such a focus on life support functions should play a more central role in biodiversity management and conservation designs, and more ecological research are needed to reveal such functional relationships, in particular in ecosystems that increasingly become humanly appropriated and exploited, such as those in urban areas.

In this paper, we focus on the roles of individual species in the provision of ecosystem services by performing functions and processes in the ecosystems they are a part of. Once there is more knowledge of these roles, there will be richer opportunities to analyze the economic significance of the existence of individual species. Hitherto, a common way to put an economic value on species has been to explore people's preferences for the existence of species (Nunes et al., 2003). While this indeed reflects that people value species' existence from an aesthetic and ethical perspective, species' functional role is taken into account only to the extent that people are aware of it. The intricate nature of these functional roles suggests that such awareness is low. However, increased knowledge of how single species perform key functions in ecosystems makes it not only possible to increase the awareness among the general public, it also creates new opportunities to value species' provision of ecosystem services such as seed dispersal, pollination or insect pest control. If it is known how such services serve as inputs into the production of goods in, for example, agriculture and forestry, production function approaches can be followed for estimating the economic value of a changed provision of the services. For example, natural insect pest control services could be valued by the estimation of yield losses in agriculture or forestry in cases of absence of natural enemies, as proposed by Östman et al. (2003). Another way to illustrate the economic significance of the services is to measure the cost of replacing them by man-made substitutes; for example, replacing pollination services performed by native bees by way of human means.

Applying production function and replacement cost approaches for estimating the economic value of ecosystem services provided by individual species generally require detailed ecological knowledge of the species. In this paper, we show how such knowledge allows an estimation of the costs of replacing a specific seed dispersal service performed by the Eurasian Jay (Garrulus glandarius). Our case is the seed dispersal capacity necessary for the regeneration of natural oak forest stands in the Stockholm National Urban Park (NUP) – a large city-park in close adjacency to Stockholm, the capital of Sweden. Our primary objective is to estimate the number of seed-dispersed oaks in the park that results from jays and to determine the costs of replacing this service through human means. What we want to accomplish by this case study is not any exact cost estimates, but rather to illustrate how ecological and economic knowledge can be combined in order to indicate the extent of an economic value of an ecosystem services that is likely to be unknown to most people (including policy makers).

The paper is organized as follows. The next section provides a descriptive background of the setting and the ecological complex in which the seed dispersal service takes place. Section 3 presents economic valuation approaches, in particular the replacement cost method, and the ecological-economic analysis resulting in replacement cost estimates. In Section 4 we conclude by discussing ways of interpreting these results as well as discuss cases and conditions when the replacement cost method may be applied in measuring economic values related to biodiversity.

2. Oak forests and the National Urban Park of Stockholm

Of central concern in this article is the process of natural oak forest regeneration in the National Urban Park of Stockholm (NUP) - a 2700-ha area located adjacent to Stockholm city (Fig. 1). Oaks have played a central role in the historical development of the cultural landscapes of this park for a considerable time. The first written regulations concerning oak harvesting dates back to the year 1347 when oaks were widely valued as a source for hard wood and for acorn production (Herdin, 2002). Before this date, farmers that managed lands within the present-day park landscape deliberately eliminated oak seedlings from their property to make way for more arable lands. At the end of the 1600s, when large parts of the park were turned into royal hunting grounds, the ruling elite deliberately favoured oak trees, mainly due to its high demand as materials for naval shipbuilding (Fogelfors and Hansson, 1997). In 1680 the Royal Djurgården Administration (RDA) was established to manage lands in the park and the royal hunting grounds[1]. The management objective was based on romantic ideals, with the foremost objective to enhance the scenic beauty of natural lands, favouring stands of broad-leaved trees, particularly oaks (Barthel et al., in review). With these ideals the Swedish kings created several English landscape parks in the 1700s, and planted broadleaved and pine forests (including exotic tree species) on partly overgrazed hunting grounds, giving the landscape much of the character that it holds today (Lange, 2000). This coincided with the era of the park successively being opened up for recreational use by the public, including

[1] RDA is still managing most of the lands in the present-day park.

the establishment of several recreational institutions (e.g., an amusement park, a theatre, and several museums). The first recorded management plan for the oak population within the park dates from the beginning of the 18th century and ever since the oak-dominated landscapes are part of the identity of the present-day park.[2]

Furthermore, the park holds an extremely high level of biological diversity[3], perhaps due to a deliberate and long-term management policy that has favoured the cultivation of oak trees (Quercus robur and Q. petrea). This has resulted in one of the largest oak forests in Sweden, belonging to the oak woodland areas around Lake Mälaren (Stadsbyggnadskontoret, 1997). On average, 18% of all trees found in the park consist of oaks (H. Niklasson, forester, RDA, personal communication, 2002), some of which are at least 500 years old (Länsstyrelsen, 1999). Since the park holds one of Europe's largest populations of giant oaks (Herdin, 2002), it is important in an international perspective, especially when considering that the epidemic oak disease seriously has lead to the decline of oak forests over wide ranges of Europe in the past two decades (Führer, 1998; Barklund, 2002). Symptoms of this disease[4] are, however, still rare among the oaks in NUP. In addition, natural regeneration rates of Quercus spp are often low, contributing to regeneration failures due to a number of factors such as an uneven quantity and quality of acorn production over time, heavy predation and

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[2] In the early 1800s up to 10.000 people a day could visit the area for recreation (Lundevall, 1997); today some 15 million annual visits are made to NUP (Wirén, 2000).

[3] Few areas of the same size in Sweden holds such high species diversity. For example, some 1000 species of butterflies, 1200 species of beetles, 250 species of birds, and over 800 vascular plants have been recorded in the park. Of red-listed species there are more than 60 insects of which 29 are listed as threatened and 27 as vulnerable, and 32 species of fungi, and several species of vascular plants, mammals, amphibians, reptiles and fish (Bråvander and Jakobsson, 2003).

[4] Typical symptoms of oak disease are weakening of the crown, high shoot and branch mortality and eventually the whole crown dies.

browsing on acorns and seedlings, and low growth rate of oak seedlings (Löf et al., 1998; Lundberg et al., in review).

The oak is also a major keystone species[5] (Paine, 1969) in the hemiboreal forest zone, producing a unique set of niches for flora and fauna that depend on old hollow trees (Ranius et al., 2001). Oaks may host up to 1500 other species of insects, mosses, fungi and lichens (Hultgren et al., 1997), and provide nesting and feeding sites for many birds and bats. Of all red-listed insects, 80% are linked to old growth oak trees and lime trees (Gothnier et al., 1999). Active management of keystone species is one of the most efficient ways of maintaining biodiversity and of building resilience in ecosystems (Colding and Folke, 1997; Colding et al., 2003).

2.1. The role of jays in natural oak forest regeneration

Although many oaks in NUP are originally planted, of which the most charismatic ones represent solitary trees in open park- and scrub lands, as much as 85% of the oaks is estimated to be a result of natural regeneration (H. Niklasson, RDA, pers. comm., nov. 2002). Studies reveal that natural regeneration of oaks in the Stockholm-region depends on an intimate chain of ecological relationships. Figure 2 summarizes the essential links of this relationship with the Eurasian Jay (Garrulus glandarius) representing the key link in this chain.

The Jay is a strongly arboreal Eurasian bird that prefers habitats with fairly dense cover of trees, scrub and woody undergrowth. Jays represent scatter-hoarding birds that collect and

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[5] Keystone species (Paine, 1966; 1969) play a major role in the structure of an ecosystem by maintaining high species diversity in a biological community. Its removal may cause drastic loss of other species in the community and changes its species composition.

hide acorns during the autumn for later consumption during the winter and spring (Lundberg et al., in review). A jay is hiding 4,500-11,000 acorns per year (Cramp, 1994; Clayton et al., 1996) of which a certain proportion never is found and consumed by the jays. These burrowed and 'forgotten' seeds facilitate regeneration of new oaks over wider spatial scales, and long-distance dispersal of acorns is entirely dependent on the dispersal pattern of the Eurasian Jay (Jensen and Nielsen, 1986; Frost, 1997). Acorns are carried from the mother tree to a suitable spot for a cache that often is located within the bird's breeding territory (Bossema, 1979). Although both wood mouse (Apodemus flavicollis) and red squirrel (Sciurus vulgaris) account for seed dispersal in NUP, their contribution is assumed to be low due to that they disseminate acorns only a very short distance from where the acorns fall from oaks (Lundberg et al., in review). Relative to acorns dispersed by Jays, these mammal-dispersed acorns also relate differently to acorn predation as well as germination. For example, Jays predominantly chose acorns that are most likely to produce viable seedlings; dispersal and burrowing of acorns by Jays also result in a reduction of post-dispersal predation and reduced exposure to harmful environmental conditions; and caches are preferentially located along edges by Jays[6] where light conditions tend to be favorable for growth, and where grazing pressure and exposure to defoliating caterpillars is low. Acorns dispersed by Jays are also buried at a suitable depth for ideal germination (Bossema, 1979). Furthermore, the annual dispersal of acorn by Jays in the wider landscape enhances the gene pool of oaks and provides insurance to disturbance across spatial and temporal scales in the region (Lundberg et al., in review).

Post-dispersal predation by small mammals on exposed acorns on the ground in pastures and deciduous forests has been found to be close to 100% (e.g. Frost 1997). Observations made by Lundberg et al. (in review) indicate that Roe Deer (Capreolus capreolus), wood mice

[6] This indicates an overall avoidance of open areas by seed predators.

(Apodemus spp.) and possibly also Badger (Meles meles) and Voles (Clethrionomus spp) predate on acorn in NUP. Hence, there is low potential survival of passively dispersed acorns (especially if physical factors such as drought, removal, and freezing are considered), suggesting that Jay behavior is critical for successful, natural oak forest regeneration.

Another critical link in the oak regeneration complex is the presence of coniferous forest. Although results show that Jays will attempt breeding in most of the forest habitats present in NUP, pairs possessing territories with a large proportion of coniferous trees are most likely to breed successfully (Lundberg et al., in review). Breeding success is positively related to the amount of coniferous forest due to nest concealment, food supply, and predation on adults (Andrén, 1990). Hence, for optimal conditions in natural oak forest regeneration, management and adequate protection of coniferous stands in NUP and surroundings areas is an important aspect.

Seed dispersers, such as Jays have been classified as mobile link species by Lundberg and Moberg (2003). Mobile link species support essential ecosystem functions by moving actively or passively among green patches and ecosystems, connecting either different patch types or similar patch types with some kind of “barrier” between them (Lundberg and Moberg, 2003). Examples include pollinators and seed dispersers, such as birds, insects, and mammals. Mobile link species are considerably important in the regeneration of ecosystems that have been disturbed by linking disturbed sites to undisturbed source areas where new organic material may be brought in to the perturbed site (Nyström and Folke, 2001; Elmqvist et al., 2003). Considering that oak disease in the future may spread to NUP, natural long-term disposal of acorns from uncontaminated (undisturbed) areas depend entirely on the presence of Jays. Hence, in this context Jays contribute to building resilience or ‘buffering capacity’ (Holling, 1973) in the oak forests of NUP and the greater Stockholm region.

3. Economic valuation of jays' seed dispersal services

The fact that many ecosystem services, e.g. jays' seed dispersal, are not priced at any market implies that special valuation methods have to be used for finding out what trade-offs people are willing to make for the sake of these services. Welfare economics suggests that such trade-offs, which in turn depend on people's preferences, measure economic values (e.g., Boadway and Bruce, 1984; Johansson, 1991; Hausman and McPherson, 1996). The valuation methods follow either of two strategies: (1) to reveal people’s trade-offs with respect to ecosystem services from their behaviour on markets for related goods (revealed preferences (RP) methods), and (2) to ask people directly about what trade-offs they are willing to make through survey instruments such as face-to-face interviews and mail questionnaires (stated preferences (SP) methods, such as contingent valuation) (Freeman, 2003).

We suggested in the introduction that changes in the provision of ecosystem services can be valued through a production function (PF) approach. Such a PF method follows an RP strategy because economic values are measured from changes in producer and consumer surpluses at the market for the product for which the ecosystem service serves as an input. In terms of species' provision of ecosystem services, this puts their functional roles in focus. In contrast, SP methods take functional roles into account only if people are (made) aware of them.

An alternative way to value species' functional role is to follow the replacement cost (RC) method, which we do in this paper. This method focuses on the costs of programs providing man-made substitutes for ecosystem services. Since society would not have to pay such costs if the ecosystem service is available, the idea is that such cost savings indicate the economic value of the service. The RC method has been used repeatedly for valuing ecosystem services, but mainly those provided by biological communities, such as wetlands, rather than those provided by individual species (Sundberg, 2004). From a welfare economics perspective, the RC method has a weakness because its basis tends to be cost data on actual or hypothetical governmental programs rather than data on market behaviour revealing people's trade-offs. However, the method still results in valid estimates of economic values if the following three conditions are met (Shabman and Batie, 1978; Bockstael et al., 2000; Freeman, 2003):

1. The man-made substitute provides functions that are equivalent in quality and magnitude to the ecosystem service.
2. The man-made substitute is the least cost alternative way of replacing the ecosystem service.
3. Individuals in aggregate would be willing to incur the replacement costs if the ecosystem service was no longer available.

We now turn to the particular oak seed dispersal service carried out by jays in NUP. The result of this dissemination of acorns is a natural regeneration of oaks in the park. We quantify this result by estimating the number of oaks in the park that spring from jays' seed dispersal. The costs of instead using human techniques for causing this number of oaks are our RC estimates.

To what extent are the three conditions above fulfilled in our application of the RC method? As to the first condition, there are human substitutes for jays' seed dispersal service available. Seeding acorns and planting oak saplings are two possible techniques. We approach the second condition on cost-effectiveness by estimating the costs of both these possible replacement techniques. Whether the third condition is fulfilled or not is uncertain, because there is no information if people have an aggregate willingness to pay that would cover the replacement costs. However, public support for preserving the NUP oak population can be expected, because of the park's importance as a recreational area and oaks being a major characteristic of the park. Hence, preserving healthy oak stands is an important management objective in this park. An additional indication of public support is the fact that NUP received formal status in law in 1995 and is governed by a specific law in the Swedish Environmental Code as an area of 'national interest' (Schantz, 2002; Barthel et al., in review). The law stipulates that new development is allowed and other measures can be taken only if this can be done without intruding on the park landscape or the natural environment and without causing harm on the landscape's natural and cultural values[7].

Our ecological-economic analysis resulting in RC estimates consists of the following steps, presented in the next five subsections:

1. Quantifying the number of oaks that are due to jays.
2. Identifying human techniques for oak regeneration.
3. Estimating costs of seeding acorns.
4. Estimating costs of planting oak saplings.
5. Concluding about the replacement cost.

3.1. How many oaks are due to jays?

The following four steps were followed for estimating the number of oaks in the park that can be regarded as a result of seed dispersal by jays:

1. Define the basal area (g_i) for one particular tree as the cross section area of a tree stem, measured at breast height, i.e. $g_i = d_i^2\pi/4$, where d_i is the tree diameter (Sveriges Skogsvårdsförbund, 1992). The total basal area (G) in an area is then obtained as the sum $G=\Sigma_i g_i$ for all trees in the area.
2. Define a forest as an area where $G \geq 10$ m^2 per ha (Sveriges Skogsvårdsförbund, 1992). Given this definition, the forest area in the park is 655 ha. On average, oaks in the

[7] The law is a result of a democratic process, partly resulting from that various non-governmental organizations and pressure groups expressed concern for the numerous exploitation projects that were planned in the park.

park account for 18% of G and not more than 85% of the oaks is considered to be a result of natural regeneration – the remaining 15% is the result of human planting.

3. Note that the just mentioned facts do not imply that a pure oak forest amounting to 655 x 0.18 x 0.85 = 100.2 ha is found in the park. The forest is a mix of different tree species. A more realistic approach is to observe that the definition of a forest implies that the oak cross-section area per ha forest in the park is at least 10 x 0.18 = 1.8 m^2. The diameter of an average full-grown oak in the park can be estimated to at least 0.2-0.25 m (H. Niklasson, RDA, personal communication, 2002), i.e. 0.225 m on average. Thus, g_i=0.04 m^2 and it follows that there are at least 1.8/0.04 = 45 full-grown oaks per ha. This indicates that the total number of naturally generated full-grown oaks in the park is at least 45 x 655 x 0.85 = 25,054.

4. Note that this number of full-grown oaks cannot be accomplished by planting 25,054 oak saplings. When oak saplings are planted in the park, ten saplings are planted in a 5x5 m square and each square is expected to result in one full-grown oak (H. Niklasson, RDA, personal communication, 2002). This suggests that there is a need to plant 25,054 x 10 = 250,540 saplings in order to accomplish 25,054 full-grown oaks.

How well does the need for 250,540 saplings correspond to what is known about the results of natural seed dispersal? In the two areas studied by Frost (1997), she found that 514 and 1,555 oak saplings per ha forest, respectively, were a result of natural seed dispersal. Multiplying the average value 1,034.5 with the forest area in the park (655 ha) results in 677,598 oak saplings. This is higher than 250,540, and one reason for this might be the fact that the calculation of the number of full-grown oaks per ha was based on the minimum value of G allowed by the forest definition.

Let us therefore consider the average (250,540 + 677,598)/2 = 464,069 oak saplings in the following. One way to accomplish this amount of saplings is to plant according to the number of first-year oak saplings that are due to seed dispersal by jays. The average number of such saplings is 54 per ha (Frost, 1997). Slightly more than 13 years are needed if this result is to be accomplished each year for every hectare until the number of saplings is 464,069 (464,069/(655x54)=13.1). Assuming a 14-year period, the average number of saplings per year is 33,148.

Is this a reasonable figure? Does seed dispersal by jays in the Park really result in 33,148 saplings per year? As described in Section 2.1, a jay is hiding 4,500-11,000 acorns per year. There are 84 jays in the park (Andersson, 2002), which means that they are hiding 378,000-924,000 acorns per year. We lack, however, data on the proportion of cached acorns consumed by the Eurasian Jay. Studies on the Blue Jay (Cyanocitta cristata), a close North American relative to the Eurasian Jay with similar acorn dispersal behaviour and functioning in natural oak regeneration, reveal that 54% of the total production of acorns is hided and that 20% of the total production is consumed (Darley-Hill and Johnson, 1981; Johnson and Atkinson, 1985). Hence, the Blue Jay consumes some 37% of all acorns hided. Assuming this relationship to hold true for the Eurasian Jay, some 63% of the hided acorns are not consumed, which implies a potential of 238,140 to 582,120 saplings per year. However, only about 50% of the acorns is likely to develop into saplings (H. Niklasson, RDA, personal communication 2003). This implies 119, 070 to 291,060 actual saplings per year, which suggests that 33,148 is not likely to be an overestimate.

3.2. Human techniques for oak regeneration

The preceding section illustrated the result of the seed dispersal service carried out by jays in the park. How can this result instead be obtained by human efforts? Three main oak regeneration techniques are used in Sweden: (1) Seeding acorns at suitable places, (2) planting oak saplings, and (3) facilitating natural regeneration (acorns drop from oaks and grow close to the trees) by, for example, increment felling, harrowing, shelterwood systems and logging (Sveriges Skogsvårdsförbund, 1992; H. Niklasson, RDA, personal communication, 2003). We have not investigated the third technique because it cannot be regarded as a substitute for jays' seed dispersal service. Jays do not only put acorns in the ground, they also provide the additional service of spreading the acorns over a large area. However, this additional service can be accomplished by the two first techniques, and they are subject to a detailed cost analysis below. The first technique is actually a kind of imitation of jay behaviour.

What technique is the most suitable one? Planting saplings seem to be relatively expensive. A cost analysis of oak regeneration on arable land in southern USA indicates that the costs of seeding acorns are just one third of the costs of planting saplings (Bullard et al., 1992). In addition, there can be substantial reductions in seeding costs if mechanical seeding can be applied instead of manual seeding (Löf and Madsen, 1998); there are examples of a 50% reduction (E. Möller Madsen, forester, Trolleholm Manor, personal communication, 2003). However, while mechanical seeding can be applied to reasonably flat and open land, manual seeding is likely to be the only feasible alternative in a wooded area such as NUP (E Möller Madsen, personal communication, 2003).

However, the relatively low costs of seeding acorns do not take into account that the result of seeding is less certain than that of planting. Löf and Madsen (1998: p. 3) conclude that ”it is doubtful whether seeding is equally reliable as planting”. Their results indicate that seeding should be avoided at places with many rodents or vermin insects or much weed. In practice, the ability of the worker to select good places for the acorns is of great importance for the result.

3.3. Costs of seeding acorns

Applying this technique would be to mimic jay behaviour by having one or several workers that are seeding acorns at suitable places in the forest. Recall that there is a need for 464,069 oak saplings, or 33,148 saplings per year in 14 years. Acorns that are purchased from nurseries can be expected to have a 60% rate of germination (Södra Fröstationen, Åbyfors, personal communication, 2003). This means that 33,148/0.6=55,247 acorns have to be seeded each year in 14 years.

This technique is used at Trolleholm manor in southern Sweden and the data used below have been obtained from E Möller Madsen, forester at Trolleholm. Seeding requires suitable preparation of the ground, and the use of a special drill facilitates the seeding. For a case when 20,000 acorns are manually seeded on one hectare, labour costs can be estimated to SEK 2,000 per ha for preparation of the ground and SEK 5,200 per ha for seeding.[8] This implies a labour cost per acorn of 7,200/20,000 = SEK 0.36 per acorn. The price of acorns are SEK 100 per kg and 1 kg contains about 200 acorns, which means that the price per acorn is SEK 0.5 (Södra Fröstationen, Åbyfors, personal communication, 2003).

This indicates that in the case of the park, the total costs for the first year of seeding amount to 55,247 x (0.5+0.36) = SEK 47,512. Ignoring discounting, this implies a total cost for all 14 years amounting to about SEK 0.67 million.[9] However, this is likely to be a substantial underestimate of the total seeding costs for two reasons:

1. The labour costs per acorn were based on a case where 20,000 acorns are manually seeded on one hectare. In the case of the Park, 773,458 acorns are in total to be seeded on

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[8] On 11 April 2005, SEK 1 corresponded to USD 0.141.

[9] Hougner (2003) presents a sensitivity analysis showing, inter alia, the consequences of using different discount rates. For example, a 5% discount rate would imply a total cost for 14 years that is about 25% lower than the undiscounted sum.

655 ha, which is likely to increase the cost per acorn due to the increased distance between each acorn. In fact, the former case implies 1 acorn per 0.5 m^2 and the latter 1 acorn per 8.5 m^2. If one assumes that each acorn is placed in the centre of squares amounting to 0.5 m^2 and 8.5 m^2 respectively, this implies that the distance between each acorn is $8.5^{0.5}/0.5^{0.5}$ = 4.1 times greater in the latter case than in the former case. SEK 0.36 x 4.1 = 1.48, which would imply a total cost for the first year of seeding amounting to 55,247 x (0.5+1.48) = SEK 109,389, or about SEK 1.53 million for all 14 years.

2. As was mentioned above, the results of seeding is relatively uncertain. This indicates that more than 773,458 acorns have in fact to be seeded in order to accomplish 464,069 oak saplings. As a consequence, we will regard SEK 1.5 million as a minimum estimate of the costs of seeding acorns.

3.4. Costs of planting oak saplings

Planting of saplings is a technique in use in NUP already today, and cost data have been obtained from H. Niklasson, forester at RDA. The labour cost for a trained worker is SEK 2,648 per day. One worker can be expected to be able to plant 600 saplings per day, which implies a labour cost of SEK 4.41 per planted sapling. The cost of one sapling can be estimated to SEK 10, which implies a total cost of SEK 14.41 per planted sapling. Recall that 33,148 saplings have to be planted each year. This implies that for the first year of planting, the total costs amount to 33,148 x 14.41 = SEK 477,663. Again ignoring discounting, this implies a total cost for all 14 years amounting to about SEK 6.7 million.

3.5. The replacement cost

Identification of a cost-effective technique is one of the conditions for the RC method to be a valid method for economic valuation. While seeding seems to be a less expensive technique, it was noted above that a total cost of SEK 1.5 million is likely to be a minimum estimate. If the costs would exceed SEK 6.7 million, planting saplings would instead be the cost-effective technique.[10]

This suggests that the minimum value per pair of jays in the park in terms of RC is about SEK 35,000 (1,500,000/42). If one instead has the costs of the more reliable but also more expensive planting technique as a point of departure, the value per pair of jays is about SEK 160,000 (6,700,000/42).

4. Discussion

We conclude that there are substantial costs involved for replacing the seed dispersal service performed by jays in NUP by a man-made substitute. While a more precise estimation of the replacement cost made in this analysis may be limited due to lack of reliable data on the caching behaviour of the Eurasian Jay, obtained results are likely to be conservative rather than the opposite, see Section 3.2. Still, a cost of SEK 1.5-6.7 million might be small enough to make an investment in a man-made substitute a viable option. Such an alternative also means managing NUP without any deliberate considerations paid to support existing jays. While such a management alternative, where humans take full responsibility for oak forest regeneration in NUP, is fully possible, it may be less advantageous in biological terms. For example, acorns do not survive storage for longer time-periods (usually not more than a year), and the continuous dispersal of acorns through space and time by jays holds genetic advantages relative to seedlings derived from artificial seed storage (Lundberg et al., in review). Perhaps most critical, replacing this service through human substitutes would be affordable only in limited areas, but costs for oak regeneration would swiftly increase when

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[10] For the sake of simplicity, we ignore combinations of the two techniques, such as seeding acorns in some parts of NUP and planting saplings in other parts.

considering oak populations at larger spatial scales in this landscape. Based on the aggregated oak forest-area in NUP of 100 ha, the average cost for natural oak forest regeneration (i.e. by jays) ranges between SEK 15, 000 to 67,000 per ha depending on the replacement technique chosen. Hence, assuming that this cost would be the same in areas outside NUP, it would be extremely high when considered at a larger spatial scale, such as in safeguarding long-term oak forest regeneration in the Stockholm region. However, such a generalization of the RC results for NUP implicitly assumes that people's concern for preserving oak populations is not restricted to NUP only.

An alternative interpretation of the obtained valuation is that it would be worth SEK 1.5-6.7 million to invest in measures that would secure the existence of jays in NUP. Sticking to the just mentioned implicit assumption, indicates that it is worth SEK 15,000-67,000 per hectare of existing oak forests in the region to maintain the seed dispersal function performed by jays. Since the park and surrounding ecosystems hold one of the largest populations of giant oaks in Europe, and that the oak represents a keystone species in this part of the world, oak forests need to be managed from an ecosystem perspective in the Stockholm region. Genetic advantages, problems involved in artificial storage of acorns, the continuous temporal and spatial oak dispersal service facilitated by jays are reasons why perfect man-made substitution is difficult to accomplish, which emphasize the conservative nature of the RC estimates. An investment in management measures of jays would help secure a continued oak forest regeneration in the park, or alternatively be invested in other existing oak forests in the Stockholm region where conditions for jays are poor. Such management measures include the safeguarding and active management of coniferous forests in the wider landscape to enhance breeding success of jays, as well as investing in measures that maintain the connections between different stands of oaks in the larger landscape, such as forested corridors used by jays when moving among different green areas. Such an alternative interpretation of results may be preferable in the event of a spread of oak disease or new pathogens (e.g. Kelly and Meentemeyer, 2002). Hence, management needs to be proactive and considers the critical aspects in the oak forest complex described in Section 2.2 to safeguard the natural renewal capacity of oak populations.

4.1 Applicability of the RC method

Most of the valuation studies of species are related to the preservation of single species, derived from applications of SP methods resulting in estimates of people's willingness to pay for avoiding the loss of a particular species (Nunes et al., 2003). One needs to recognize that such expressions of economic values do not reflect the value of those ecosystem services associated with biodiversity that the general public is not informed about or has no experience with. For example, for applying a SP method to the Euroasian Jay, a questionnaire needs to be designed comprehensively enough to convey detailed information on the life support functions and processes related to this species. Hence, SP methods may not always be the best choice due to the complexity involved of accurately and comprehensively communicating these relationships in a survey (Nunes et al., 2003). However, such methods are useful for finding out the value attributed to species by people on aesthetical and ethical grounds.

The RC method tends to be applied for assessing services related to whole biological communities, such as wetlands, rather to those related to particular species.[11] This is not

[11] For example, Samarakoon and Abeygunawardena (1995) and Gunatilake and Vieth (2000) assessed the replacement cost of soil erosion in Sri Lanka, and Kim and Dixon (1986) assessed this in Korea; Xue and Tisdell (2001) valued the replacement costs for forest ecosystem services provided in a nature reserve in China; Folke (1990) valued the replacement techniques for a Swedish wetland system; Leschine et al. (1997) assessed wetland flood protection capacity in Washington; Chichilnisky and Heal (1998) estimated the water purification

surprising, because ecologists know very little about what functions particular species hold in particular ecosystems, and more ecological research is needed in identifying which species play a major role in the structure, dynamics, and stability in local ecosystems. The RC method (given due account taken to the conditions stated in Section 4) and the PF method may nevertheless be the most preferable economic valuation method in cases where species perform key life support functions and processes, such as seed dispersal, pollination, or pest regulation, and when knowledge of these functions and processes is low among people or difficult to communicate to them. As demonstrated in this article, the RC method is useful for valuation of services provided by mobile link organisms. Where known functional relationships include both mobile link organisms and keystone species, such as the oak–jay complex described in this article, PF or RC methods are highly motivated due to high biodiversity benefits in a successful preservation of keystones. Similar complexes involving mobile links and keystones have been described elsewhere in the ecological literature, although not framed in this context. For example, different species of *Ficus* are known to be pivotal for the maintenance of tropical biological diversity (Gilbert, 1980; Terborgh, 1986). Among others, figs are a critical resource for the survival of birds, bats, squirrels, and monkeys during the dry season when wild flowers and other fruits are low in abundance. In turn, many fig-feeding species act as seed dispersers of Ficus (and of other tree species); hence, these mobile link species are critical for regenerating barren places (Pereira and Seabrook, 1990) and for the renewal of Ficus in the wider landscape, and in particular ecosystems that have been disturbed. Investing in management and preservation measures of such mutual, functional relationships in ecosystems is not only important at the species-level,

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service by the watershed in Catskill mountains, New York; and Spurgeon (1992) valued the replacement costs for ecosystem services provided by coral reefs.

but at the landscape-level (Colding and Folke, 2001). Hence, in the light of that the oak represents a keystone species in NUP, jays' seed dispersal service results in important indirect biodiversity benefits due to the multitude of organisms that are dependent on oaks. Investing in measures and practices that safeguard the presence of jays, and thus also a successful regeneration of oaks, is in this sense highly productive. The RC estimates suggest that investments in NUP of at least SEK 35,000-160,000 per pair of jay are economically motivated. These are minimum figures partly because the RC estimates are conservative in themselves and partly because they do not account for any values attributable to jays due to aesthetical or ethical considerations.

Similarly, the value of native, unmanaged, bee communities could be subject to an RC analysis of man-made pollination or the cost paid for rents of domesticated honeybees (Apis mellifera) temporarily used to provide pollination on crop fields during bloom. Derived RC estimates can motivate the minimum extent of investments in, for example, safeguarding critical native pollinator habitats adjacent to crop fields (Kremen et al., 2004). Investing in such measures may not only promote the chances for a continued generation of ecosystem goods, such as crop-pollinated foods, but also provide other biodiversity benefits. As was shown in the study by Östman et al. (2003), RC analysis may also be applied to motivate management costs for natural enemies that predate on insect pests in agriculture.

In a world of limited financial resources, costs for managing ecosystems and natural resources need increasingly also include measures that support and preserve organism groups that perform key life support functions and processes in ecosystems – largely a neglected aspect in environmental conservation and management designs. Mobile link organisms, pest regulation species, and potentially other organism groups represent such groups of organisms. It should be mentioned, though, that a severe limitation for successful applications of PF or RC methods to estimate biodiversity benefits is that sufficient data are often not available.

For our RC analysis, we were fortunate to have a necessary set of ecological and economic data, including specific data related to the seed dispersing behavior of Jays, detailed land cover data pertaining to oaks in NUP, and estimates of costs related to man-made substitution techniques for oak forest regeneration. However, with increasing ecological knowledge of key functions and processes performed by species, PF and RC studies may become more widely applied in the future and become an important tool in determining appropriate management measures and policies related to biodiversity.

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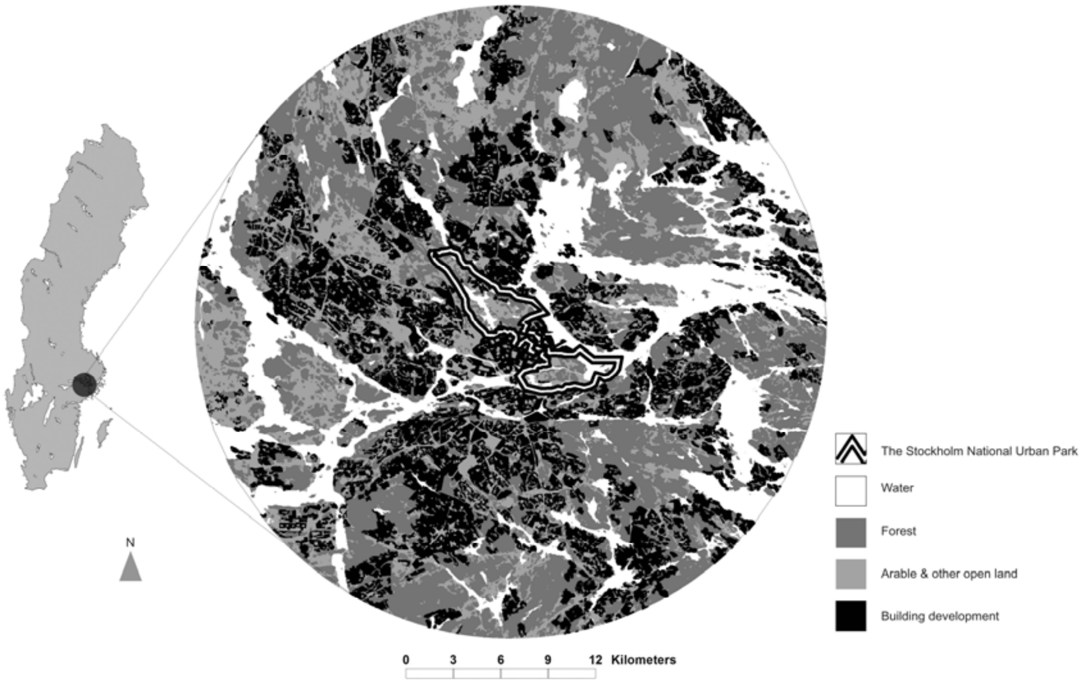
List of figures

Figure 1. The National Urban Park in central Stockholm. Composed of a mosaic of different ecosystems, the park forms the largest green area structure of the Northern and Eastern parts of Stockholm city, the capital of Sweden.

Figure 2. The natural oak forest regeneration complex. This complex is necessary to consider in natural regeneration of the oak-dominated landscape in the National Urban Park (NUP). Oak forest regeneration depends on Siberian jays for dispersal and planting of acorns. In turn jays depend on the presence of dense coniferous forests for egg laying and for hiding offspring from predators. Hence, in order for successful natural oak forest regeneration in NUP, it is not only critical to preserve jay populations but also coniferous forest stands within or in close proximity to NUP.



N
The Stockholm National Urban Park
Water
Forest
Arable & other open land
Building development
0 3 6 9 12 Kilometers

Fig.1

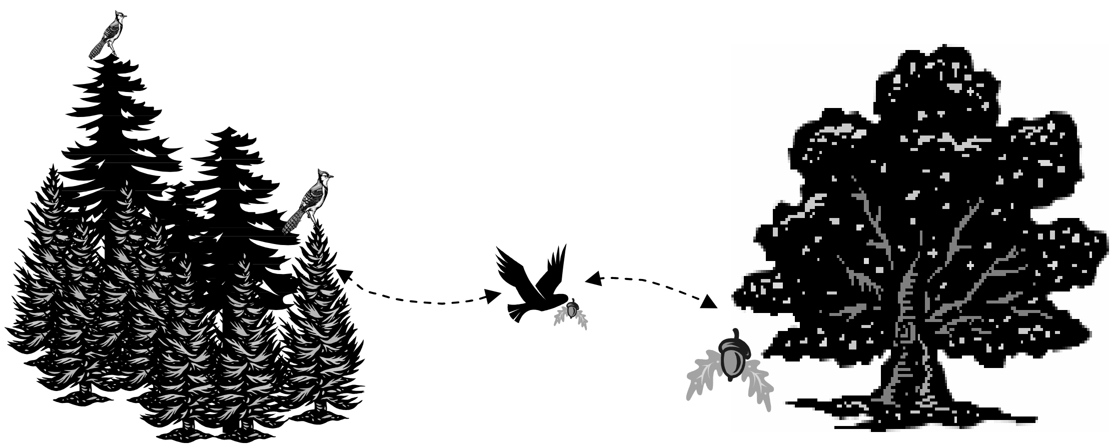


Fig. 2