

Estimating population size of a nocturnal burrow-nesting seabird using acoustic monitoring and habitat mapping

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Abstract

Population size assessments for nocturnal burrow-nesting seabirds are logistically challenging because these species are active in colonies only during darkness and often nest on remote islands where manual inspections of breeding burrows are not feasible. Many seabird species are highly vocal, and recent technological innovations now make it possible to record and quantify vocal activity in seabird colonies. Here we test the hypothesis that remotely recorded vocal activity in Cory's shearwater (*Calonectris borealis*) breeding colonies in the North Atlantic increases with nest density, and combined this relationship with cliff habitat mapping to estimate the population size of Cory's shearwaters on the island of Corvo (Azores). We deployed acoustic recording devices in 9 Cory's shearwater colonies of known size to establish a relationship between vocal activity and local nest density (slope = 1.07, $R^2 = 0.86$, $p < 0.001$). We used this relationship to predict the nest density in various cliff habitat types and produced a habitat map of breeding cliffs to extrapolate nest density around the island of Corvo. The mean predicted nest density on Corvo ranged from 6.6 (2.1–16.2) to 27.8 (19.5–36.4) nests/ha. Extrapolation of habitat-specific nest densities across the cliff area of Corvo resulted in an estimate of 6326 Cory's shearwater nests (95% confidence interval: 3735–10,524). This population size estimate is similar to previous assessments, but is too imprecise to detect moderate changes in population size over time. While estimating absolute population size from acoustic recordings may not be sufficiently precise, the strong positive relationship that we found between local nest density and recorded calling rate indicates that passive acoustic monitoring may be useful to document relative changes in seabird populations over time.

Keywords

Cory's shearwater, *Calonectris borealis*, vocal activity, nest density, Random Forest, Azores, Macaronesia, Procellariiformes

Introduction

Seabirds are globally the most threatened group of birds (Croxall et al. 2012), and assessing the severity of threats or the effectiveness of conservation measures requires periodic assessments of population size to understand whether populations are declining or increasing. Estimating population trends remains challenging for many seabird species due to logistical constraints imposed by often inaccessible breeding locations on remote islands. In addition, several seabird species nest in burrows or cavities, and are active in breeding colonies only during the hours of darkness. For these nocturnal burrow-nesting seabirds visual assessments of population size are not possible, and robust estimates of population size are usually based on marking a large number of birds (Sanz-Aguilar et al. 2010; Sutherland and Dann 2012) or estimates of burrow occupancy (Pearson et al. 2013). On many islands the marking of seabirds or inspection of burrows is logistically not feasible, because birds nest on inaccessible cliffs. As a consequence of the various logistical constraints, the population sizes of many species of storm-petrels, petrels, shearwaters and alcid are very poorly known (Brooke 2004; Croxall et al. 2012). The burrow-nesting habit of many species, which directly influences the complexity of population assessments, also contributes to their vulnerability to invasive alien predators, a key threat to seabirds (Croxall et al. 2012; Jones et al. 2008). Thus, the group of species for which assessments of population size are critical is also one of the most difficult to monitor.

Monitoring the population size of nocturnal burrow-nesting seabirds has recently benefited from autonomous acoustic recording devices, which can be deployed on remote islands to record the vocal activity of seabirds (Buxton and Jones 2012; Buxton et al. 2013; McKown et al. 2012; Borker et al. in press). Acoustic recording is a promising approach for many biodiversity assessments (Celis-Murillo et al. 2012; Penone et al. 2013; Sueur et al. 2008; Wimmer et al. 2013), and has been successfully employed to assess the changes in seabird breeding populations following island restoration (Buxton et al. 2013). The number of recorded seabird vocalisations is expected to increase in larger colonies, but to our knowledge no attempt has been made to estimate absolute population size of a nocturnal burrow-nesting seabird species based on vocal activity rates measured from acoustic recordings.

Here we present a case study for estimating the population size of Cory's shearwater (*Calonectris borealis*, recently split from *C. diomedea* (Sangster et al. 2012)) nesting on a rugged island in the Azores archipelago in the North Atlantic Ocean. The Azores are estimated to hold a significant proportion of the Cory's shearwater world population, with a breeding population between 49,500 and 89,000 pairs (Monteiro et al. 1996).

All populations are affected by introduced predators (Fontaine et al. 2011; Hervías et al. 2013), but for most islands it is unknown whether populations are declining or stable because no quantitative estimates of population size exist. Robust population size estimates are a key knowledge gap for the protection of seabirds in the Azores (Ramírez et al. 2008). To address this knowledge gap, we deployed acoustic recording devices in Cory's shearwater colonies of known size to calibrate the relationship between vocal activity and local nest density. We used this relationship to predict the nest density at other recording stations where a count of occupied nesting burrows was not possible. We further produced a habitat map of breeding cliffs and extrapolated nest density around the island of Corvo based on the habitat composition of breeding cliffs. This approach yielded the first quantitative estimate of the breeding population of an island that is believed to hold one of the largest Cory's shearwater populations in the world (Furness et al. 2000; Granadeiro et al. 2006; Monteiro et al. 1996).

Methods

Study area

Corvo is a small (1700 ha) island of volcanic origin located in the central North Atlantic (39°40'N, 31°7'W). The volcanic cone of the island rises to 718m, and due to wind and wave action much of the volcanic cone has eroded, particularly on the western coast. The erosion has led to almost vertical cliffs between 200–600 m tall along the majority (16.3 km) of Corvo's coastline. Due to the inaccessible nature of the cliffs, the size of the Cory's shearwater population has never been quantified (Furness et al. 2000), but based on counts of birds rafting offshore it has been estimated that 6000–12,000 pairs or 30,000 individuals nest on the island (Monteiro et al. 1996; Ramírez et al. 2008).

Acoustic recording and nest density assessment

In May 2011 and 2012, we deployed a total of nine autonomous acoustic recorders (SongMeter SM2, Wildlife Acoustics Inc., Concord, MA) in colonies that were expected to have varying nest density of Cory's shearwaters, but where all burrows and potential nest cavities within a 50 m radius could be manually inspected to assess local nest density. These colonies were situated on Corvo as well as on the islands of Faial (38°35'N, 28°48'W), and Vila Franca do Campo (37°42'N, 25°26'W) in habitats similar to the cliffs on Corvo. In May 2012, we deployed 12 additional acoustic recorders in various cliff habitats on Corvo where nest density assessment was not possible, including near-vertical cliffs where recorders were deployed with ropes. All recorders were deployed in wind-sheltered areas on the ground or a cliff ledge, with two independent microphones elevated 30 cm above ground and spaced < 50 cm apart.

Recorders operated on an identical schedule for the entire breeding season (late May to mid October), with 1 min recordings every 10 min from local sunset to local sunrise. Gain on both independent microphones was set to the default of +42.0 dB and sound was recorded at a sample rate of 16 kHz in stereo.

In June 2011 and 2012, we searched for occupied shearwater burrows within a 50 m radius of the nine accessible recorders, based on the assumption that SongMeters can record vocalisations up to 50 m away (Buxton and Jones 2012). All potential burrows and rock cavities were inspected with a burrow-scope, and those containing an adult bird or an egg were considered as occupied and monitored for a different project (Hervías et al. 2013). The nest density around the nine accessible acoustic recorders was therefore known.

Acoustic data processing and calibration

Vocal activity of burrow-nesting seabirds at colonies is dependent on many environmental factors and thus varies considerably within nights and over the breeding season (Bretagnolle et al. 2000; Granadeiro et al. 2009). Instantaneous vocal activity is therefore unlikely to accurately predict nest density, which has affected acoustic population assessments made by human observers in the past (Bolton et al. 2010). To reduce variation in vocal activity and increase correlation between vocal activity and nest density we first excluded data from time periods when calling rates were expected to be lower and more variable, and averaged the calling rate over the remainder of the breeding season as a single metric of vocal activity per recorder location. Specifically, we discarded recordings from September onwards when thermally independent chicks require less attention by their parents and attendance and vocal activity at the colony decreases (Granadeiro et al. 1998; Magalhães et al. 2008; Paiva et al. 2010). Further, we limited recordings to 22:00–01:00 hrs local time and moon phases where < 75% of the moon was illuminated to capture the periods when vocal activity around the colony was most consistent (Granadeiro et al. 1998; Hamer and Read 1987; Mougeot and Bretagnolle 2000). Nonetheless, the attendance cycles of Cory's Shearwaters at colonies are cyclic and not all of the variation in attendance and vocal activity can be explained by the factors described above (Mougin et al. 2000). The main advantage of autonomous acoustic recorders to overcome such unexplained variation is their ability to record vocal activity consistently over long time periods and thus average out short-term variation in attendance or vocal activity patterns (Buxton and Jones 2012). After having excluded the data with lower or more variable vocal activity described above, we used the mean number of Cory's shearwater vocalisations in all remaining 1 min recordings from late May until the end of August as metric of vocal activity around each recorder.

Due to the long deployment period, the recorded vocal activity could not be assessed manually but required an automated call recognition algorithm (Brandes 2008; Digby et al. 2013; Rempel et al. 2013; Swiston and Mennill 2009). We performed automated analyses of all field recordings with the eXtensible BioAcoustic Tool (XBAT,

<http://www.xbat.org>), a bioacoustic analysis software package for MATLAB that includes algorithms for detecting sounds of interest in acoustic recordings. Specifically, we used an image processing technique known as spectrogram cross-correlation to detect and classify sounds in our field recordings that were correlated with the spectral characteristics of typical Cory's shearwater vocalizations (Mellinger and Clark 2000). To assess the effectiveness of this detection algorithm we created a control dataset from field recordings obtained in June and July 2011 in which we manually marked all shearwater calls. We then measured the performance of the detection algorithm by comparing the detected calls to the known calls in the control dataset. The detection algorithm was accurate in that > 88% of the calls detected were actual shearwater calls. In addition, the template detected 57% of the total number of manually identified calls in the control dataset. We applied this detection algorithm to all acoustic recordings, and manually audited all positive recognitions to remove erroneous classifications of background noise as Cory's shearwater vocalisations. This process resulted in a minimum number of Cory's shearwater vocalisations for each 1-min recording file.

To calibrate the relationship between local nest density and vocal activity, we used the nine accessible recorders where local nest density was known. Because we expected vocalisations to increase linearly with nest density, we fitted a linear regression to the mean number of shearwater calls per minute with nest density as dependent variable. This linear relationship was then used to predict local nest density at the remaining 12 recorders that were placed in locations where nest burrows could not be manually surveyed.

Cliff habitat mapping

To be able to extrapolate local nest density assessed via acoustic recorders to the entire suitable nesting area for Cory's shearwaters on Corvo, we adopted a habitat modelling approach to predict nest density in different cliff micro-habitats following similar work in mountainous areas (Oppel et al. 2004). We took digital pictures of the cliffs from a boat while circumnavigating the island to create a habitat map of the near vertical cliff habitat. Pictures were taken at 90 sampling points spaced 140-180 m apart and 300 m from the shoreline to ensure wide overlap in the field of view between adjacent sampling points. The pictures were then merged into composite images of the cliffs surrounding the island with the software GIMP 2.7 (Immler 2010).

The composite cliff panoramas were visually inspected and homogenous areas of similar habitat type were manually delineated as polygon features in a geographic information system (ArcMap 10.1, ESRI Inc., Redlands, CA). Each delineated polygon was given a value for three habitat features (Immler 2010). Habitat features were selected for the unique cliff environment of Corvo and the burrow-nesting habits of Cory's shearwaters (Furness et al. 2000; Ramos et al. 1997). We classified habitats based on inclination (< 60°; 60–85°, and > 85°), rock type (flat without ledges, cracks, or crevasses; broken rock with ledges, furrows, cavities; no rock), and soil layer (very shallow layer of soil unsuitable for burrow excavation; deep enough for burrow excavation).

The same three habitat features were also recorded around the location of each acoustic recording device. This allowed us to use the estimated nest density inferred from the recorded calling rate in a habitat model to predict the nest density in relation to the three habitat features, and thus assess density in those combinations of habitat features where no recorder had been placed.

Extrapolation of breeding population size

We first estimated the local nest density for all recording units based on the acoustic calibration relationship described above. We then related the estimated nest density at each recorder to the three habitat features to establish a predictive relationship between the level of each habitat feature and nest density (Pearson et al. 2013). Because we had only a small dataset to train this model ($n = 21$ recorder locations with estimated nest density), we used a powerful machine-learning algorithm based on ensembles of regression trees (Random Forest) to predict nest density for each combination of habitat features that existed along the coast of Corvo (Cutler et al. 2007; Hochachka et al. 2007; Olden et al. 2008). We used the R package 'randomForest' to construct 2500 regression trees, and used this model to predict nest density in all habitat types along the cliff. This habitat-specific nest density prediction required prediction to new combinations of the three habitat features, as only 9 of the total of 17 different combinations of the habitat features were present in the recorder data used to construct the Random Forest model. However, each level of our habitat features was represented at 3–14 recorder locations, and our predictions therefore did not extrapolate into unknown sampling space, but merely interpolated into the inferred sampling space where predictions are generally more reliable (Zurell et al. 2012). To assess whether the habitat model reliably predicted nest density we performed a cross-validation. This cross-validation tested whether a model constructed without a given recorder would adequately predict the nest density based on the habitat data at that recorder location. We then correlated the predicted nest density from the habitat model with the nest density at that recorder and concluded that our model was able to predict nest density at habitat types that were not present in our training data if there was a significant positive correlation.

To extrapolate from nest density to total population size of Cory's shearwaters, we used the habitat feature map derived from digital photographs to calculate the proportion of the entire cliff area that was covered by polygons with each combination of habitat features. The proportion of each habitat type was multiplied by the entire area of suitable cliff habitat around Corvo, estimated from the length of the coastline (16.3 km) and the height of cliffs to be 490 ha.

We then summed the number of shearwater nests predicted to occur in each habitat across the entire island to derive an estimate of island-wide breeding population size of Cory's shearwaters. We present the estimate of breeding population size with 95% confidence intervals derived from the linear regression predicting nest density around each recorder.

Results

The mean calling rate per 1-min recording ranged from 0.7 to 55.2 Cory's shearwater calls at the nine recorders with known local nest density, and from 0–25.1 calls at the recorders placed at inaccessible cliff locations. We counted between 8–56 occupied Cory's shearwater burrows in a 50 m radius around accessible recorders, and found a relationship that indicated a linear increase in local nest density with increasing calling rate (slope = 1.07, $R^2 = 0.86$, $p < 0.001$; Fig. 1). Based on this relationship, the mean predicted nest density around the 12 recorders where no nest count had been feasible was 9.5 nests/ha (95% confidence interval 4.1–18.5 nests/ha).

The 21 acoustic recorders were placed in nine different combinations of the three habitat variables and represented all levels of the three habitat features. The Random Forest habitat model relating estimated nest density to habitat features performed well in cross-validation and observed and predicted nest densities were positively correlated (Pearson $r = 0.73$, $p < 0.001$). This model predicted that nest density across all combinations of habitat features on Corvo ranged from 6.6 (2.1–16.2) to 27.8 (19.5–36.4) nests/ha (Table 1).

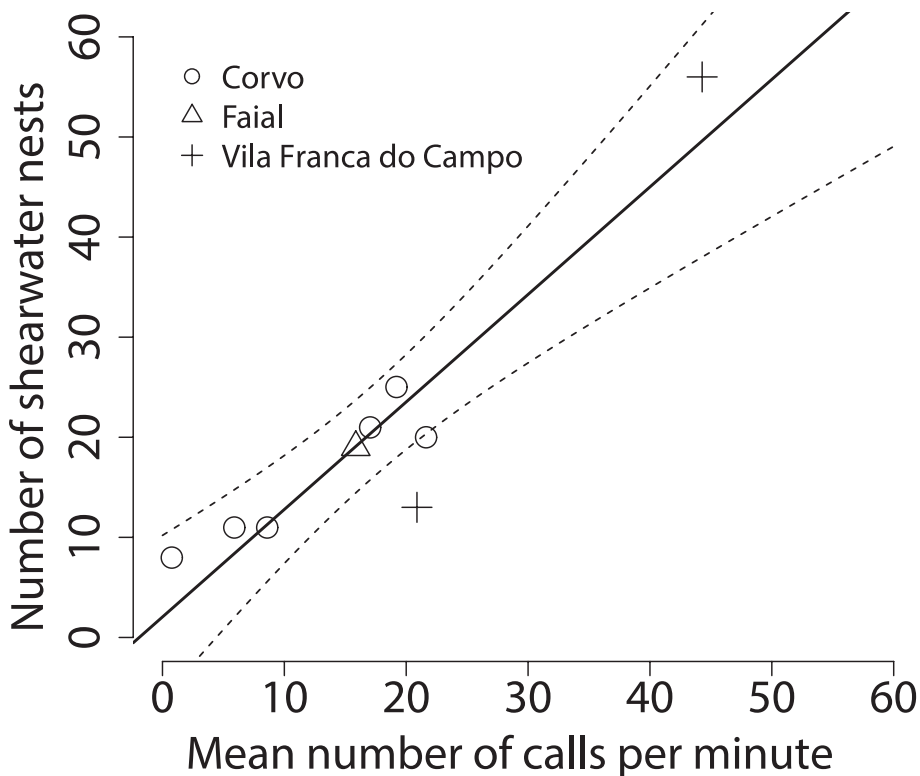


Figure 1. The number of occupied Cory's shearwater nests within a 50 m radius around acoustic recording devices increased with mean shearwater call rates measured during the 2011 and 2012 Cory's shearwater breeding seasons (solid line = linear regression with slope = 1.07, $R^2 = 0.86$, $p < 0.001$; broken line = 95% confidence intervals). Different symbols represent data from three islands in the Azores, North Atlantic Ocean.

Table 1. The distribution of estimated nest densities and number of estimated Cory's shearwater nests (with 95% confidence intervals) around the 490 ha of cliff habitat on the island of Corvo (Azores) in 2012.

| Soil Type | Rock type | Inclination | Area (ha) | Nest density (nests/ha) | N nests |
|-----------|-------------|-------------|-----------|-------------------------|-----------------|
| deep | flat rock | <60° | 2.2 | 27.8 (19.5–36.4) | 62 (43–81) |
| deep | flat rock | >85° | 3.8 | 23.5 (15.9–31.9) | 89 (60–120) |
| deep | broken rock | <60° | 45.1 | 23.3 (17.2–30.3) | 1050 (776–1367) |
| shallow | flat rock | >85° | 3.9 | 23.1 (15.9–31.2) | 90 (62–121) |
| shallow | flat rock | <60° | 1.8 | 22.1 (14.8–31) | 40 (27–56) |
| deep | flat rock | 60–85° | 2.3 | 17.1 (10.4–26.6) | 40 (24–62) |
| deep | broken rock | >85° | 82.4 | 16.7 (11.2–24.4) | 1378 (923–2012) |
| deep | no rock | <60° | 3.3 | 16.3 (9.2–24.7) | 54 (30–81) |
| shallow | flat rock | 60–85° | 0.2 | 15.5 (9.4–24.9) | 4 (2–6) |
| shallow | broken rock | >85° | 5.3 | 13.8 (8–22) | 72 (42–116) |
| shallow | broken rock | <60° | 71.2 | 13.4 (7.9–22) | 955 (565–1565) |
| deep | no rock | >85° | 1.7 | 12.5 (6.3–20.9) | 22 (11–37) |
| shallow | no rock | <60° | 89.8 | 11.1 (5.2–20.1) | 1001 (466–1808) |
| deep | broken rock | 60–85° | 92.5 | 10.3 (5.8–19.3) | 949 (541–1785) |
| deep | no rock | 60–85° | 2.6 | 8.2 (3–17.4) | 21 (8–45) |
| shallow | no rock | 60–85° | 35.8 | 6.7 (1.9–16.2) | 241 (68–581) |
| shallow | broken rock | 60–85° | 42.6 | 6.6 (2.1–16.2) | 283 (88–691) |

Highest nest densities were predicted either on vertical cliffs (> 85° inclination) with flat rock, or in less steep areas (< 60°) with deep soil suitable for excavating burrows. Lowest nest densities were predicted in areas with intermediate inclination (60–85°) and no flat rock (Table 1). Extrapolating the estimated habitat-specific densities across the entire cliff area of Corvo resulted in an estimate of 6326 Cory's shearwater nests (95% confidence interval: 3735–10,524).

Discussion

Based on acoustic recording and habitat mapping we estimated that >6000 pairs of Cory's shearwaters nested on Corvo in 2012. This population size estimate is surrounded by considerable uncertainty (3735–10,524 pairs), which describes the potential range of the Cory's shearwater population on Corvo. Due to this large uncertainty our estimate is unlikely to serve as a useful baseline for assessing moderate changes in population size.

Our population size estimate is of a similar magnitude as previous extrapolations for Corvo (6000–12,000 pairs in 1996), which were derived from counting individuals rafting at sea or multiplying average breeding densities by the area of available habitat (Monteiro et al. 1996; Ramírez et al. 2008). Up to 15,000 individual Cory's shearwaters can be regularly observed rafting close to Corvo during the breeding season, but raft counts of shearwaters typically include a large number of non-breeding

birds (Feio and Monteiro 1998). Nonetheless, these raft observations indicate that the order of magnitude of our population estimate is realistic. The nest densities recorded or estimated in this study were at the lower margin of the densities presented by Monteiro et al. (1996; 20–60 nests/ha) and much lower than nest densities recorded for Cory's shearwaters along the cliffs of Selvagem Grande (283 ± 57 nests/ha), the largest Cory's shearwater colony in the world (Granadeiro et al. 2006). The Cory's shearwater population on Corvo thus appears to be smaller and nest at a lower density than the breeding populations in the Selvagem archipelago, despite being the largest colony in the Azores (Furness et al. 2000). It is possible that the Cory's shearwater population on Corvo may have been much larger in the past (Bolton 2001; Monteiro et al. 1996), as introduced cats (*Felis catus*) and rats (*Rattus rattus*) continue to affect breeding success of seabirds on many islands in the Azores (Fontaine et al. 2011; Hervías et al. 2013).

The large uncertainty in our abundance estimates is a consequence of error propagation across two different model predictions – the predicted nest density based on recorded calling rate, and the predicted overall abundance extrapolated from the predicted nest density per habitat type. Additional uncertainty may arise because nest density may vary due to social attraction and the presence of invasive predators in addition to suitable habitat (Igual et al. 2007; Major and Jones 2011). While more intensive calibration work with more recorder locations across an exhaustive habitat gradient and more precise habitat mapping might lead to tighter relationships between recorded calling rate and nest density, and between predicted nest density and habitat features, such intensive work is likely not realistic for the majority of remote islands for which population assessments of nocturnal burrow-nesting seabirds are required.

Despite the imprecise population size estimate, our work suggests that there is a positive relationship between calling rate recorded by autonomous acoustic recorders and seabird nest density. This finding builds on previous work (Brandes 2008; Buxton and Jones 2012; Buxton et al. 2013; Borker et al. in press) and suggests that acoustic recording may offer a practically feasible approach to monitor relative population changes of nocturnal burrow-nesting seabirds on remote islands. Continuous developments in hardware and data management (McKown et al. 2012) as well as automated call recognition algorithms (Digby et al. 2013) will make acoustic monitoring a useful tool for many remote seabird breeding colonies. Based on our work we are doubtful that the absolute size of seabird populations can be estimated with sufficient precision and accuracy based on acoustic recordings alone. Nonetheless, because the recorded calling rate of shearwaters increased with local nest density in our study, we believe that vocal activity recorded with autonomous acoustic recorders can be used as an adequate index of population size for long-term monitoring or assessing the effects of island restoration (Buxton et al. 2013). Such an approach relies on fewer assumptions than our extrapolations of population size, and may therefore be more reliable for long-term monitoring. However, using the recorded calling rates as an index of colony size would still rely on some critical assumptions, particularly that the number of non-breeding individuals present at the colony is similar between years

and that the calling rate increases in a linear or otherwise predictable fashion with nest density. Although not evident in our dataset, acoustic recordings in very large and dense seabird colonies may overload any call detection algorithm if too many calls are recorded simultaneously. Thus, there may be an upper limit of vocal activity beyond which any further increase in colony size can no longer be detected with currently available acoustic devices and data processing algorithms. We encourage researchers working at accessible seabird colonies to employ acoustic monitoring simultaneously to traditional monitoring approaches to establish whether temporal trends in population size can be detected using acoustic monitoring.

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An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin

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Abstract

Forest management intensity often affects biodiversity, ecosystem processes and ecosystem services. To assess the influence of past management intensity on current ecosystem properties, management intensity must be quantified in a meaningful and reproducible approach. Here we developed the simple yet effective Forest Management Intensity index (ForMI), which is based only on inventory data of the living stand, stumps and dead wood. The ForMI is the sum of three components taking into account: 1. the proportion of harvested tree volume (Iharv), 2. the proportion of tree species that are not part of the natural forest community (Inonat) and 3. the proportion of dead wood showing signs of saw cuts (Idwcut). Each component ranges between 0 (no sign of management) and 1 (intensive management). Our analysis suggests that the ForMI can be used to assess management intensity in Central European forests for the last 30 to 40 years, depending on decay rates of stumps and dead wood. Our approach was tested using data of 148 forest plots of 1 ha in size in Germany. We found a significant distinction between plots that were previously described as managed and unmanaged as well as between plots comprising tree species of the natural forest community and those with additional, introduced coniferous tree species. We conclude that the index is applicable to a wide range of forest management types, but should not be misinterpreted as an index for old-growth structure.

Keywords

Land-use intensity, Biodiversity exploratories

Introduction

Forest management intensity is suggested to be a main driver of biodiversity, ecosystem processes and ecosystem services (Fischer et al. 2010, Gustafsson et al. 2012). To assess the influence of past management intensity on current ecosystem properties, management intensity must be quantified in a meaningful and reproducible approach. Here we are concentrating on influences of silvicultural forest management at the stand level, which represents impacts at the ecosystem level. So far, there is no straightforward and agreed approach for its quantification. The main challenge in developing such an index of forest management intensity is to incorporate the different elements of forest management that affect stand structure and composition and to quantify these. Recently, approaches have been suggested that require theoretically derived variables, which are not directly related to a particular forest stand in question (Luyssaert et al. 2011, Schall and Ammer 2013). Schall and Ammer (2013) provided an extensive review on concepts and approaches for assessing land-use and specifically forest management intensity to provide the scientific basis for their approach. We believe that the two previous approaches produced indicators of forest management intensity that are not entirely transparent, not easy to quantify, and not strictly or exclusively related to human pressure on forest ecosystems; see Niemeijer and de Groot (2008) for a discussion of properties of useful environmental indicators. Here we propose an alternative approach, the index of Forest Management Intensity (ForMI), which is derived from stand inventory data of living trees, stumps and dead wood. The ForMI is the sum of three components taking into account: 1. the proportion of harvested tree volume (*Iharv*), 2. the proportion of tree species that are not part of the natural forest composition (*Inonat*) and 3. the proportion of dead wood showing signs of saw cuts (*Idwcut*). In the following we provide the rationale for constructing the index from these three components.

One core activity of forest management consists of the harvest of living trees. There are a variety of silvicultural approaches leading to even-aged forest stands characterized by distinct age-classes or uneven-aged forest stands resulting from selection cutting. Despite the large differences between those silvicultural approaches the result is always the removal of wood. Unfortunately, the records about the amount of wood volume removed are often not specific at the stand level but are documented for compartments or management units, and not all assortments may be traced; e.g. firewood may not be recorded. However, tree removals are traceable by tree stumps left after cutting. To gain a relative measure of the amount of harvested tree volume, the difference between the observed standing volume to the maximum volume based on the self-thinning relationship for a particular age and tree species (Spellmann et al. 1999) may be used (Luyssaert et al. 2011, Schall and Ammer 2013). One major drawback of this approach is the reliance on a theoretical maximum stand carrying capacity, which is influenced by site conditions and tree species. Since these relationships are mainly established for mono-specific and even-aged stands, mixed and uneven-aged stands are rather poorly described (Pretzsch 2009). In addition, these approaches neglect disturbances, which may have affected a particular stand and influenced the difference between a potential

and the actual wood volume. The indices of Schall and Ammer (2013) and Luyssaert et al. (2011) are therefore not a direct measure of the harvesting intensity for a particular forest stand and they do not distinguish between human pressure and natural reductions in standing tree volume. Thus we propose to quantify the proportion of wood that has been removed over a period of time that is still indicated by the stumps. This is a direct expression of human pressure, as is often used in environmental indicator sets (Niemeijer and de Groot 2008), on the particular forest ecosystem in question.

In addition to harvesting, the composition of tree species is one of the main factors influenced by forest management. Although preindustrial forest management and land use change may have altered the natural tree species composition already, there is no doubt that the shift in tree species composition following the early industrial period towards secondary forests comprising coniferous species (*Picea abies*, *Pinus sylvestris*) in Central Europe has had a profound influence on forest ecosystems (Bohn et al. 2004, Ellenberg and Leuschner 2010). This element of the index therefore considers the influence on ecosystem properties and processes triggered by human-induced changes of tree species composition. Introduced tree species may change the habitat for herbivores and their predators (e.g. Gossner and Ammer 2006), the disturbance dynamics because they are more susceptible to certain disturbance factors (e.g. Albrecht et al. 2012), or ecosystem nutrient cycling and soil properties (e.g. Binkley and Giardina 1998) to name a few of such alterations. Here we refer to “natural” or “non-natural” tree species as those, which are, or are not, part of the potential natural vegetation (Tüxen 1956) that would occur as an expression of soil and climate at the observed site

Since in actively managed forests, wood is regularly removed, both the quantity and quality of dead wood are substantially altered when compared to unmanaged forests (Jonsson et al. 2005). At the same time, dead wood is of critical importance for many ecosystem functions (Harmon et al. 1986), of which the most relevant are C sequestration (e.g. Litton et al. 2007, Kahl et al. 2012), nutrient cycling (Brunner and Kimmins 2003, Kuehne et al. 2008), and provision of habitat for wood-dwelling organisms (Lonsdale et al. 2008, Rondeux and Sanchez 2010). For example, in Germany, 56% of all forest Coleoptera are dependent on dead wood (Köhler 2000). Consequently, the amount of standing and lying dead wood has been adopted as one of the Pan-European Indicators of sustainable forest management (MCPFE 2002). However, since the quantity of dead wood is highly variable in managed as well as in unmanaged forests of Central Europe (own data), it is unlikely to be a good indicator for forest management intensity. While in long-term unmanaged forests, large quantities of dead wood will accumulate (Christensen et al. 2005), this may not occur in the short-term, in particular when harvesting ceases at a time of stand development, when little dead wood is created through processes, such as self-thinning or disturbances (Harmon 2009). For example, an intensive harvesting operation may leave large quantities of dead wood if the utilization standards are low. Taking this into account, and in order to keep dead wood quantity as an independent variable for further statistical analysis, we selected a variable that is largely independent of dead wood quantity but describes its quality by means of its origin. Forest management generally tries to avoid

the natural death of trees since this would reduce the quality of the products or the amount of harvestable wood volume. This in turn leads to a decrease of dead wood originating from natural mortality of trees. At the same time in managed forests, more dead wood originates from the cutting of trees and therefore shows saw cuts. Hence we used the proportion of dead wood with signs of saw cuts as the third component of the proposed index.

In the following, we present the definition of the proposed ForMI and show an application to a set of 148 forest plots as well as a comparison with two other indices that have been calculated for the same plots.

Methods

Definition of ForMI

The first component of the index *I_{harv}* describes the proportion of harvested tree volume. Our approach is based on the assumption that the sum of the living standing tree biomass (1), harvested tree biomass removed from the stand (including the logging waste in the stand) (2), and the dead wood biomass of trees that died naturally (no chain saw cuts) (3) can be used as a proxy for the potential cumulative merchantable volume (Pretzsch 2005) at a given stand age. This approach makes the assumption of a theoretical maximum stand carrying capacity redundant and is independent of site quality, previous disturbances and tree species composition. Cut stumps are used to derive estimates of the harvested volume.

The main drawback of this approach is the uncertainty about the time until the stumps and dead wood are decayed. The decay rate of stumps depends mainly on tree species, site conditions and size (Shorohova et al. 2012). For southern Finland stump turn-over times of 61, 56 and 43 years for pine (*Pinus sylvestris*), spruce (*Picea abies*) and birch (*Betula* spec.), respectively, were found (Shorohova et al. 2012). In the case of European beech (*Fagus sylvatica*), which is the dominant deciduous tree species in Central Europe, we assume that the stump turnover time is similar to the turnover time of logs, about 54 years (Kahl et al. 2012). These values should be considered as maxima for the longevity of stumps and a time of 30 to 40 years seems realistic for the probability to find remains of cut stumps. Cut stumps of Central European tree species, such as oak (*Quercus* spec.), which are known to be more decay resistant, would add a bias to this stump-based approach. Stump size (diameter) seems to have only little influence on stump turnover time. No influence of size on stump turnover time was found for *Picea abies* in Sweden (Melin et al. 2009). The same was true for stumps of *Picea abies* and *Pinus sylvestris* in a study in Finland, while the turnover time of *Betulus* spec. stumps in the same study slightly increased with size (Shorohova et al. 2012). In addition, contradictory results have been reported for the influence of diameter on the decay rate of wood. For example, decay rates for dead wood of *Picea abies* increased (Næsset 1999) or decreased with increasing diameter (Brown et al. 1996). Regarding these studies we

believe that stump size is far less important for stump turnover time than may be assumed. Since stump turnover time is the most critical point in this context, we suggest restricting this approach to regional scale comparisons of forest management intensity to minimize the influence of climate on decomposition rates of stumps.

Although stump turnover time maybe highly variable, this approach has the advantage that the influence of tree harvest recognisable as stumps virtually decays with time. Harvesting events that occurred recently can be fully considered, whereas harvesting events that date further back will have increasingly less influence on this measure, which presumably also reflects a decreasing legacy influence. The harvested tree volume determined in this way is certainly less accurate than could be derived from repeated inventory or detailed, stand-based harvesting records, however, in most cases these do not exist. So the sum of harvested volume, dead wood volume and the living volume provides the proxy for the potential cumulative merchantable volume of the last 30–40 years.

The *Iharv* is calculated as the ratio of harvested volume to the sum of standing, harvested and dead wood volume. A value of 1 represents a clear-cut site, where tree regeneration has not yet reached the minimum tree diameter limit used for inventory purpose and no dead wood occurs, and a ratio of 0 means that no tree harvest occurred within the last 30–40 years. The index *Iharv* can only be applied, where conventional forest management using chain saws or a harvester leaves stumps. In general it can be said that all parameters (e.g. tree species, size, climate) that increase stump turnover time will also increase the component *Iharv*.

The component *Inonat* is a measure for the volume proportion of non-natural tree species. It is estimated as the proportion of harvested, living and dead wood (without saw cuts) volume of non-natural tree species to the sum of harvested, living and dead wood (without saw cuts) volume of all tree species. Again here, the legacy of former stand conditions (e.g. a cohort of introduced spruce trees that were harvested within a time frame of 30–40 years prior to assessment of forest management intensity in a forest composed now entirely of tree species belonging to the natural forest vegetation) is taken into account. A value of 1 means that the whole stand consists of non-natural tree species, whereas a value of 0 is a stand composed of tree species belonging to the natural forest vegetation only.

The component *Idwcut* represents the proportion of dead wood volume with saw cuts to the total amount of dead wood volume. A value of 1 means that all dead wood originated from management activity (wood residue) or that trees that died by natural causes were cut and used, while a value of 0 means that all dead wood is a result of natural tree death. In case where no dead wood occurs but clear signs of management are visible e.g. due to fuel sampling or in plantation forests with whole tree harvesting we recommend to adjust the *Idwcut* to a value of 1.

The forest management index ForMI is the sum of all three components *Iharv*, *Inonat* and *Idwcut*. Although the relative importance of each component as an indicator of forest management intensity is debatable, we decided to weigh each component by a value of 1. For example, a ForMI of 3 would apply to a clear-cut stand of non-natural

tree species, where no dead wood of natural origin occurs. A value of 0 would apply to a stand, where no stumps were found, only natural tree species and only dead wood without saw cuts occur. The ForMI describes strictly past management intensity and does not aim to describe forest structure or level of oldgrowthness (c.f. Bauhus et al. 2009). This is due to the fact that stand age and absolute stand volume do not play a role. A value of 0 could equally apply to a 20-years-old stand in an early successional stage after a stand-replacing fire or as primary successional vegetation on a river bank, but it also could represent a 500-years-old primeval forest.

Application of ForMI

To test our approach, we used inventory data of the 150 forest experimental plots of the German Biodiversity Exploratories (Fischer et al. 2010). The 1 ha (100 m × 100 m) sized plots are equally distributed in three exploratories representing the regions: Schwäbische Alb (Alb), Hainich-Dün (H-D) and Schorfheide-Chorin (S-C). The predominant silvicultural systems and forest management types in each region were considered. These produce even-aged coniferous stands (*Picea abies*, *Pinus sylvestris*), even-aged beech (*Fagus sylvatica*) stands, uneven-aged beech stands, and even-aged oak (*Quercus spec.*) stands. In addition, there are extensively managed or unmanaged beech-dominated forests. The even-age stands are later referred to as age-class forest. The inventory data of the living stands are based on a plot inventory (500 m²) carried out in 2008 and 2009 (Fischer et al. 2010, Hessenmöller et al. 2011). Dead wood inventories were conducted in 2012 using a stratified sampling design with all standing and downed dead wood >25 cm being recorded on the 1 ha plot (volume calculations based on Meyer 1999) and downed dead wood >7 cm and <25 cm being estimated using the line intersect method (Warren and Olsen 1964, Van Wagner 1982) with two perpendicular transects of together 270 m length. Information on saw cuts and dead wood volume was then used to calculate the *Idwcut*. Stumps > 7 cm diameter were estimated on 2 m wide strips along the same transects, which served as central line of the strips. The area covered by these strip-transects was 522 m². Volume of harvested trees was calculated based on allometric functions (Muukkonen 2007). Data of 148 plots were available for this analysis. The new index ForMI was compared with the existing land use and disturbance intensity (LUDI) approach by Luyssaert et al. (2011) on all available 148 plots and with the Silvicultural Management Index (SMI) by Schall and Ammer (2013) on a subset of 30 plots. All analyses were performed in R 3.0.2 (www.r-project.org).

Results and discussion

The ForMI provided a clear distinction between managed and unmanaged forests (Wilcoxon Test $p < 0.001$) (Fig. 1). The main difference between managed and unmanaged forests was caused by the low number of stumps and the low amount of dead wood

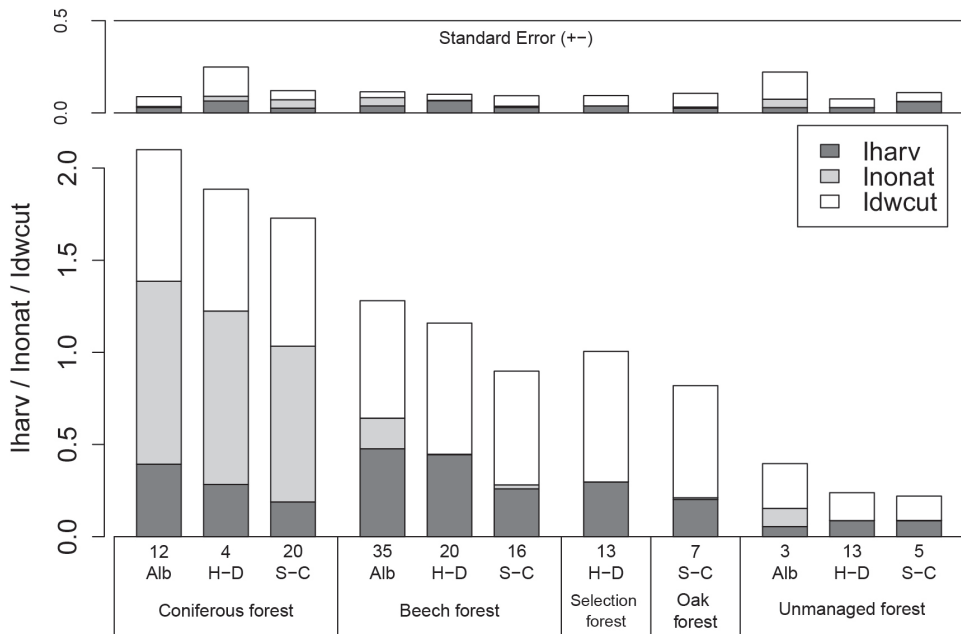


Figure 1. Distribution of the forest management intensity index ForMI and its 3 components across 5 different forest management types in the Biodiversity exploratories Schwäbische Alb (Alb), Hainich-Dün (H-D) and Schorfheide-Chorin (S-C). Numbers below the bars indicate the number of plots per group. The second bar plot above shows the standard error for each component. In the exploratories Alb and H-D, coniferous forest comprises even-aged *Picea abies* stands, and in the S-C exploratory *Pinus sylvestris* age class forest. Beech forest in all exploratories refers to even-aged *Fagus sylvatica* stands. Selection forest in the H-D exploratory is uneven-aged selection cutting stands dominated by *Fagus sylvatica*. Oak forest in the S-C exploratory is even-aged *Quercus* spec. forest. Unmanaged forest in the Alb exploratory represents extensively managed *Fagus sylvatica* forest, in the H-D and S-C it has been unmanaged for 10–60 years.

with saw cuts in unmanaged forests. Four out of 21 unmanaged stands had a ForMI of 0, which suggests that they have been unmanaged for at least 30–40 years. This result is congruent with other information about these unmanaged forest plots (Fischer et al. 2010). The largest contribution to the high ForMI value of coniferous forests was attributable to the *Inonat* component, which is close to 1 in mono-specific coniferous forests. The three variables of the ForMI presented here were calculated based on the volume of living, harvested and dead trees. For the calculation of *Iharv* and *Inonat* also the use of basal area was tested for 29 selected plots. Because basal area of dead wood could not be estimated, *Iharv* was calculated based on harvested and standing tree volume only. A comparison based on a linear model between the ForMI based on volume calculations as predictor variable and the basal area approach as predicted variable shows that both yield comparable result ($a=0.97$, $b=0.13$, $p<0.001$, $R^2=0.97$).

The ForMI as well as its three components cover the whole range of values across the 148 experimental plots (Fig. 2). The distribution of *Iharv* is right-skewed indicat-

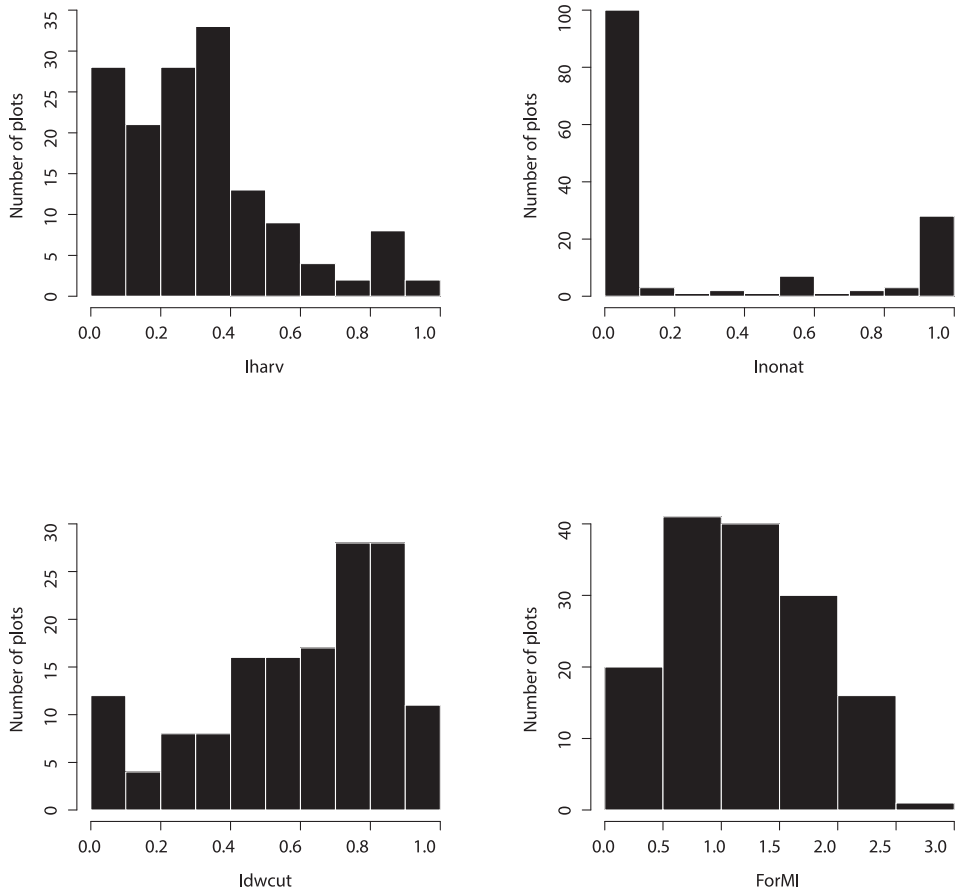


Figure 2. Distribution of the forest management intensity components: *Iharv* - proportion of harvested volume; *Inonat* - proportion of non-natural tree species; *Idwcut* - proportion of dead wood volume with saw cuts; and of the combined *ForMI* - forest management intensity index. Total number of forest plots is 148.

ing that only few plots experienced rather intensive recent harvest. The distribution of *Inonat* shows a bimodal shape with two maxima, one at 0 (only natural tree species), reflecting the dominance of beech plots among the exploratories, and one at 1 (only non-natural tree species) and only few stands, where these two tree species groups occur together. *Idwcut* shows a left-skewed distribution indicating that in most stands dead wood has been created by harvesting activities. The distribution of *ForMI* is slightly right-skewed and peaks at a value of 1. No relationship between *Iharv* and *Inonat* was found while there were significant positive, but not strong relationships between *Idwcut* and *Iharv* and between *Idwcut* and *Inonat* (Fig. 3)

Schall and Ammer (2013) proposed the Silvicultural Management Index (SMI), which is composed of a tree species-specific risk and a density component. In their rationale, tree species selection affects among other things the susceptibility of forest

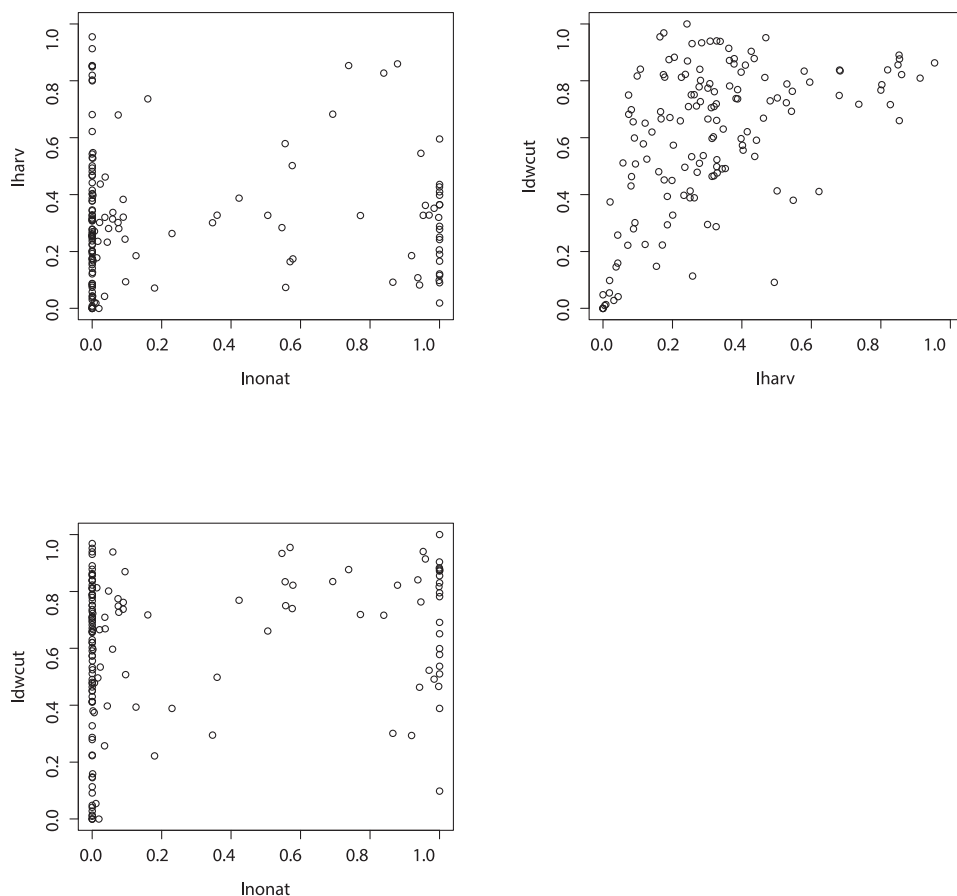


Figure 3. Relationships between the three components of the forest management intensity: *Iharv*, *Inonat* and *Idwcut*. Spearman rank correlation between *Iharv*-*Inonat* ($p=0.64$, $r_s=0.04$), *Idwcut*-*Iharv* ($p<0.001$, $r_s=0.5$) and *Idwcut*-*Inonat* ($p=0.01$, $r_s=0.21$)

stands to natural disturbances. With increasing susceptibility, management intensity, e.g. through thinning or harvesting, must be more frequent to reduce the risk of stand loss. In Central Europe the susceptibility to disturbance tends to be higher for secondary coniferous than for natural hardwood forests. Consequently, the risk component of Schall and Ammer (2013) is to some extent comparable to the *Inonat*, and their density component to the *Iharv*. The SMI approach was applied to a subset of 30 plots of the Biodiversity exploratories. A comparison based on a linear model between the SMI and the ForMI shows that both indices yield comparable results ($p<0.001$, $R^2=0.72$). A comparison of the ForMI with the land use and disturbance intensity (LUDI) approach by Luyssaert et al. (2011), which is based on the same 148 plots used by us, showed that these indices do not converge and obviously capture different attributes of forests. The LUDI is based on the difference between the potential and the actual biomass storage and does not consider the intensification of forest management that

is expressed by the change in tree species composition. Across all forest management types there was only a low although significant linear correlation ($p < 0.001$, $R^2 = 0.07$). For plots dominated by non-natural coniferous tree species (*Picea abies*, *Pinus sylvestris*, $n = 36$), no significant correlation was found ($p = 0.28$) while those plots dominated by hardwood species, such as *Fagus sylvatica* and *Quercus* sp. ($n = 112$), had a significant correlation ($p < 0.001$, $R^2 = 0.41$).

The advantage of the ForMi is its simple yet effective approach, which allows the calculation based only on volume or basal area inventory data of the living stand, stumps, and dead wood. No additional assumptions and models with regard to maximum stand carrying capacity or risk potential have to be employed. The ForMI approach proved to be applicable to all observed silvicultural management systems and allows their direct comparison. Although we have not examined yet how different silvicultural management systems, such as clear-cutting or coppice with standards, or large-scale disturbances, such as storm damage or fire, may affect ForMI, we believe that this index is applicable across the whole range of forest management types, except when trees are harvested including their root stock. The disadvantage of the ForMI is that the assessment of harvesting intensity depends on the visibility and longevity of stumps, and that it does not take into account the management frequency and is therefore not useful to describe situations where management occurs in long time intervals that exceed the longevity of stumps, as may be the case in tropical lowland rainforests.

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Why do some institutional arrangements succeed? Voluntary protection of forest biodiversity in Southwestern Finland and of the Golden Eagle in Finnish Lapland

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Abstract

Despite global, regional, and national policy efforts, biodiversity is on the decline worldwide. The purpose of this paper is to explore the critically important institutional and social features of those economic instruments that in practice motivate beneficiaries and stakeholders to protect biodiversity. The paper presents two case studies: the natural values trading (NVT) scheme in southwestern Finland and the protection of the golden eagle (*Aquila chrysaetos*) in Finnish Lapland. NVT builds upon the voluntary actions of landowners, payments for ecosystem services, and a fixed-term period of protection (ten years). The protection of the golden eagle is based on tolerance payments. This paper combines legal studies and institutional economics to abduct the reasons underlying the success of both cases. In both cases, institutional entrepreneurship promoted the confidence of stakeholders and beneficiaries in the schemes and the consequent trust amongst the agents encouraged the actors to modify their behaviour.

Keywords

Environmental law, Institutional economics, Biodiversity conservation, Economic instruments: Payments for ecosystem services, Pragmatism

Introduction

In recent years, economic instruments for biodiversity protection have regained their lustre as the concept of ecosystem services has gained attention amongst governments, civil societies, and the media. Ecosystem services have rapidly become the mainstream means by which to describe the benefits of nature (ecosystems, biodiversity) to society. This concept is now used for many purposes (Gómez-Baggethun et al. 2010), such as estimating the economic value of ecosystems and justifying the use of market-based instruments for biodiversity conservation (TEEB 2010, MEA 2005). A wide variety of payments for ecosystem services (PES) schemes are used around the world (Ten Brink et al. 2011). Most PES schemes reward actors who enhance or maintain ecosystem services (Jack et al. 2008) and in some cases, a PES scheme is intended to reverse behaviour or activities that negatively influence the ecosystem service (Hiedanpää and Bromley 2014). Schemes may also encourage the creation of habitats or otherwise ecologically valuable areas (Bullock et al. 2011). In different circumstances different institutional arrangements seem to work (Farley and Costanza 2010).

In most payment schemes, a government pays for ecosystem services (Engel et al. 2008). However, not much is known about the social preconditions and institutional conditions of economic instruments that in practice motivate stakeholders and beneficiaries to act for biodiversity. Our purpose here is to report two cases that have motivated policy makers, stakeholders and beneficiaries to participate in biodiversity protection. The first case is the natural values trading (NVT) scheme in southern Finland (Gustafsson 2008, Hiedanpää and Bromley 2012), and the second is the protection of the golden eagle (*Aquila chrysaetos*) in Finnish Lapland (Ollila and Ilmonen 2009).

Natural values trading

The launch of the Natura 2000 nature conservation programme in 1997 attracted unprecedented attention in northern Satakunta. As a culmination, four local forest owners went on a hunger strike to protest how the reserve network had been planned, saying that their opinions had not been considered and that social and cultural considerations and values had been completely side-lined in the planning process. Their campaign attracted nationwide attention, including personal visits by the Minister of the Environment and the Minister for Agriculture and Forestry. As a consequence, the boundaries of some of the sites were redrawn (Hiedanpää 2002).

The idea of NVT was first floated in the mid-1990s by Raimo Hakila. First principles of it were drafted during the development phase in 2001–2002. The phase gave credence to the idea that NVT was indeed a viable approach to tackling the problem of forest biodiversity, even at the national level (Hakila 2002). It was put to a practical test as part of the Finnish Biodiversity Programme for Southern Forests, METSO, in 2003–2007. To set the experimental phase in motion, a collaborative steering group was founded involving five key regional organisations and administrators: Regional Forestry

Centre, Regional Environment Centre, The Central Union of Agricultural Producers and Forest Owners (MTK), Finnish Private Forest Owners Association, and the Finnish Association for Nature Conservation in Satakunta. Funding for the project (€400,000 annually) comes from the Ministry of the Environment and the Ministry of Agriculture and Forestry. The NVT pilot project was extended to the whole of southwestern Finland in 2005 and was completed in 2007. In 2008, NVT was introduced in the Act on Financing Sustainable Forestry (Law on the Financing of Sustainable Forestry 544/2007). However, the key principles envisioned in the local regulatory experiment for NVT differed substantially from what was eventually adopted in southwestern Finland.

In essence, NVT, as it was tested as part of the METSO programme in 2003–2007, provides forest owners in certain ecologically valuable areas with a voluntary choice between producing natural values or timber. There were two buyers in NVT: the Regional Forest Centre and the Regional Environment Centre. The eligible sellers included all those forest owners (in total 45 000) in southwestern Finland who had sites and habitats in their forests that meet the specified criteria. Local municipalities and businesses are not parties to NVT because they are not eligible for benefits under the Act on the Financing of Sustainable Forestry. The contracts have terms of ten years; they are not agreements in perpetuity.

It was preferable that the contract sites fulfilled the Biological Nature Conservation Criteria (BNCC). The criteria are based on the forests structures and dynamics important for biodiversity and valuable forest habitats. Forest structures include, e.g. coarse woody debris, burned wood, old individual stands of hardwood and other deciduous trees, especially aspen. The criteria for certain forest habitat types include firstly primary criteria for identifying the forest habitat and its representativeness, secondly criteria for landscape ecological location and area, and thirdly complementary criteria for additional biodiversity values. Forest habitats include forests in a natural or semi-natural stage, forested mires, hardwood swamps, herb-rich forests, rich heath forests, and semi-natural grazed forests. (Ministry of the Environment 2003, 71.)

During the experimental phase, from 2003 to 2007, 158 contracts were signed. The contract area covered 1,520 hectares, 1,193 hectares of which fulfilled the BNCC. The average size of the area covered by the contracts was 8.8 hectares. The average payment was €155 per hectare per year, whereas on the sites that did not fulfil the biological criteria, the average payment was €31 per hectare per year. In total, 356 land owners committed forestland to NVT. There were more sites offered than accepted and more sites than contracts, although some contracts covered more than one site. However, every contract covered sites that fulfilled the biological criteria. Most of the contracts were agreed upon because there was decaying wood on the site; that is, old, dry, peaty forest. Managerial conservation actions were included in 35 of the contracts (Gustafsson 2008, 15).

Golden eagle compensation scheme

The golden eagle has been protected in Finland since 1962, when the population had declined to between 20 and 50 pairs. Since then, conservation efforts have led to a

substantial recovery of the species. In 1999, there were 175 known nesting territories. However, the recovery of the species has led to a conflict between species conservation and reindeer husbandry (Suvantola 2013).

Because the golden eagle preys on reindeer calves, the conservation of this species has been in conflict with reindeer herding in Finnish Lapland (Ollila and Ilmonen 2009). To ease this conflict, a new scheme that seeks to provide an incentive for reindeer owners to tolerate the eagle was implemented in 1999. Under this scheme, reindeer owners receive compensation based on the headcount of the species, not based on damage caused in individual cases, as was the case previously (Reply of the Parliament of Finland 228/1997). The initial idea for the scheme was based on a similar scheme implemented in Sweden, in which compensation for losses caused by wolverines is based on estimated killings rather than on damage caused in individual cases.

The Ministry of the Environment then began to develop the scheme, and the core idea of the Swedish model was taken as a point of departure. The preparation of the golden eagle compensation scheme continued as collaboration between the Ministry of the Environment and the Forest and Parks Services. The proposed design was then discussed with the representatives of the Sami people, the Association of the Reindeer Co-operatives, the Regional Environmental Centre of Lapland, and a representative of the individual reindeer owners. Consultations led to amendments to the proposal and the final scheme. For example, the golden eagles nesting in neighbouring countries were taken into account. It was clear from the beginning that to gain acceptability, the design and implementation of the golden eagle compensation scheme would require strong co-operation among the stakeholders.

The golden eagle compensation scheme was implemented in 1999 (Council of State Decision 373/1999, later replaced by Council of State Decree on Compensation of the Losses Caused to Reindeer Husbandry by the Golden Eagle 8/2002). In conjunction with the adoption of the scheme, a negotiating group was set up. The group consists of the representatives of the Forests and Parks Services, the Regional Environmental Centre of Lapland, the Association of the Reindeer Co-operatives, the Sami Parliament, the Finnish Game and Fisheries Research Institute, and the Ministry of the Environment (Below 2000). The purpose of the group is to monitor on-going research on the effects of large predators on reindeer husbandry to make it possible to assess the accuracy of compensation (Government decree 1077/2011).

The incentive scheme is based on information about the golden eagle's known nesting territories (Suvantola 2013). There is an annually revised compensation rate for an occupied territory. Currently (in 2013), the rate is €694 (amendment 566/2012). In mountainous areas, the payment for an occupied territory is twice the standard rate (Government decree 8/2002 4 §). This higher payment is based on empirical studies that indicate that golden eagles prey more on reindeer in mountainous areas. If a golden eagle pair produces offspring in its territory, the compensation is three times the standard rate in forest areas and five times the standard rate in mountainous areas (Government decree 8/2002 3, 4 §). The purpose of these terms is to cover the additional prey of the species needed to feed the offspring. It also aims at providing a

continuing incentive as the amount of compensation increases with increased nesting and reproduction of the species.

The financial payment is made to individual reindeer co-operatives (Government decree 8/2002 6 §). If it can be proven that a golden eagle has killed a reindeer belonging to an individual reindeer owner, the co-operative must compensate the owner for the value of the reindeer (Government decree 8/2002 7 §). Otherwise, the co-operative decides how to use the annual payments. For example, the funds can be divided among the reindeer owners who have suffered losses, or the funds can be used for collectively beneficial projects, such as product development or meat production facilities (Suvantola 2013). This is the key difference compared to the Swedish model, where the payments are made to the political Sametinget, the Sami Parliament (Sellethin and Skogh 2004). The Swedish model was developed to increase the equitability of the scheme. By making the payment to those co-operatives where the territory of the golden eagle is situated, the occurring costs of the conservation are more likely to be met (Suvantola 2013).

Approach and materials

Our empirical task is to analyse the social preconditions and institutional conditions underlying the motivational success of these cases. We define success not only by positive ecological outcomes but also by positive social, cultural and political outcomes. These instruments have been viewed as acceptable and legitimate amongst those affected and, consequently, have had positive effects on how biodiversity and its protection have been perceived (Paloniemi and Varho 2009, Horne et al. 2006, Suvantola 2013).

Nevertheless, both schemes are intended to provide incentives for biodiversity protection rather than merely relying on traditional direct regulation that prohibits certain types of activities and punishes violations. However, we argue that also other features have contributed to the success of these governance experiments leading to wider effects on biodiversity governance in Finland. Identifying some of the critical similarities and differences between these two cases should enable us to reach conclusions concerning the critical conditions for the institutional and regulatory design of nature conservation that motivates beneficiaries and stakeholders to participate and act.

The approach taken in this study is a combination of institutional economics (Bromley 2006, Hodgson 1998) and legal studies (Posner 2003), with a strong emphasis on pragmatism (Talisce and Aikin 2011, Dickstein 1998).

In institutional economics, pragmatism implies that “[i]ndividual habits both reinforce, and are reinforced by, institutions. Through this circle of mutual engagement, institutions are endowed with a stable and inert quality. Further, institutions play an essential role in providing a cognitive framework for interpreting sense-data and in providing intellectual habits or routines for transforming information into useful knowledge” (Hodgson 1998, 171). Habits – the repertoires of potential actions that sustain life – develop and change in environmental transactions that happen within

and between institutional, social and technological domains (Dewey 1988, Herrmann-Pillath 2013; Hodgson and Knudsen 2013).

In legal studies, pragmatism implies that the approach to law is instrumental. Law is seen as an instrument used to achieve societal objectives by creating new formal conditions to change habits that are considered problematic (Posner 2003). Legal pragmatism entails that policy making is understood as a process of institutional experimentation (Hoffman 2011, Bulkeley and Castán 2012). From the point of view of research, pragmatism entails an empirical and abductive approach (Cooke 2006, Haack 2009).

Our research materials consist of legal and policy documents and scientific literature concerning both cases. In addition, we have applied qualitative research methods, namely, theme interviews and participant observation. The first author participated as an observer at the meetings of the NVT steering group (Punch 2005, 183). Between July 2003 and August 2006, the NVT joint group convened on 20 occasions. The author systematically documented every statement made at these meetings, recording verbatim what was said and taking note of the drift and tone of the argument. These meetings constitute the most important empirical material for understanding the NVT case. He interviewed five members of the NVT collaborative steering group in August 2005. The focused interviews addressed NVT and the organisational and institutional changes that NVT had brought about in the region of Satakunta. The second author conducted two interviews with the key persons behind the golden eagle compensation scheme in 2012. One was the practical contributor and the other the legal advisor of policy maker. The themes of the interviews included the birth of the instrument, the process of making it an instrument, and the functioning of the scheme.

The following result section is a thick description (Geertz 1973) of the institutional and social ground of these two instruments and policy experiments. Following the logic of abduction (Paavola 2004), the discussion section constitutes *the case*, i.e. we answer to our theoretical research question how habits and more formal institutions got stabilized.

Results

Defining natural values

NVT

The collaborative steering group soon recognised that for natural values to become tradable goods, they had to be identified and itemised apart from their environment. The identification and definition of natural values for the purposes of NVT is based on the biological nature conservation criteria (BNCC) specified in the METSO program (Ministry of the Environment 2003). These criteria are effectively functional and structural characteristics of the environment that are considered valuable from a biodiversity point of view. No laws or other official norms stipulate the value or the requirement to protect the NVT sites. Habitats of special importance (as specified under

section 10 of the Forest Act) and conservation areas designated under section 25 of the Nature Conservation Act are not eligible to be NVT sites.

In NVT, a natural value is owned by the person who owns the land that features a valuable structural or functional characteristic. From the landowner's point of view, NVT refers to a fixed-term contract concerning a certain land area, such as a patch of old-growth forest. In this way, the natural value becomes a transferable private commodity that the landowner can either sell or withhold from selling. Therefore, the state-as-buyer is primarily interested not in the land itself but rather in the ecosystem services produced by that biologically valuable patch of land. In other words, the natural value of the land is an intangible public commodity that the state wants to conserve.

The BBNC were adopted in the NVT scheme. However, these criteria have not been rigorously applied in every transaction, although the collaborative steering group has allowed for local exceptions, and the ministries have not objected. In this way, landowners have effectively been involved in defining the criteria upon which ecological characteristics have been defined as tradable commodities and the prices paid for them. In cases in which the conservation criteria have not been met but NVT contracts have been signed, the areas concerned have either been close to a nature conservation area or have been part of some other valuable habitat or the contract has involved management or restoration measures aimed at increasing biodiversity at the site.

The collaborative steering group decided that the prices of natural values would be determined based on losses sustained from forgoing timber production. In addition, payment was done for the natural value of the site and any forest management measures undertaken. Once the pilot project was underway, the emphasis shifted rapidly from the compensation of losses from forgoing timber production to natural values. The prices of these values were based on the surface areas of valuable habitats, standing trees, and the structural ecological characteristics of natural values. The latter included exposed decaying wood, burned wood, and broad-leafed deciduous species, especially aspen. Management measures are compensated for according to the Act on the Financing of Sustainable Forestry. The government has also contributed by declaring income from NVT to be tax exempt.

Instead of a fixed price table, the collaborative steering group created a five-tiered pricing framework for forest structures to help determine the economic value of each NVT site. The forest owner's tendering price could be higher or lower than that indicated by the pricing framework. If the asking price was higher, the forest owner was asked to give reasons for her or his price. No reason was needed if the price was lower, but the forest owner needed to be informed that he or she could have received a higher price. The referendary had a 15 per cent bargaining leeway in either direction. The price paid for natural values could not exceed the top level, but it could be lower than the lower limit.

Golden eagle

In Finnish legal culture, wild animals have been regarded as *res nullius*, nobody's property (Määttä 1999, Francione 1995). Wildlife is part of nature, and the related risks

are natural risks, which in principle are borne by private actors. Therefore, it could be argued that the state is not legally bound to pay compensation for losses caused by wildlife. By definition, monetary payments for “natural” losses are *subsidies* that the state pays voluntarily rather than compensation that the state has a legal duty to pay. However, it has also been argued that by protecting the damage causing species the state has removed the right of the people to defend themselves and their property against these natural risks and thus, the state could be held as liable for covering the losses caused by protected species (de Klemm 1996).

It is rational for the state to cover such damages; otherwise, those who suffer harm from wild animals would have an incentive to harass or kill the species that cause damage. The way in which the state compensates for the damage is relevant. By choosing the compensation measure, the legislature can regulate behaviour, habits, and perceptions regarding biodiversity protection. In the case of the golden eagle, the legislature created an incentive for conservation by paying for the natural values instead of for the damage caused by the species.

Previously, the presence of the golden eagle only created an economic burden for reindeer owners; now, they have an opportunity to gain economic benefit from the presence of the bird. This argument was used to convince the reindeer owners to commit to the scheme (Ollila and Ilmonen 2009). Under the verified damage compensation scheme, the golden eagle represented a loss of income and additional work for reindeer owners; under the incentive scheme, however, a found nest represents income. As the reindeer owners receive compensation each year, regardless of what damage has occurred, there is also an incentive to focus on protecting the reindeer rather than poaching or harassing the golden eagle. This behaviour is rational for both reindeer husbandry and conservation of the golden eagle.

Attuning the organisations

NVT

Raimo Hakila took an active role in exploring new alternative approaches to protect and produce natural values. During the experimental phase, he was on the payroll of the Satakunta branch of the Central Union of Agricultural Producers and Forest Owners (MTK) (Hakila 2006). This type of activity is unusual for someone in his position as a well-known nature conservationist. Hakila wanted to arouse enthusiasm about the idea of NVT among landowners and their interest groups because the success of the project would ultimately depend on their commitment. His efforts eventually paid off as the opposition between conservation and protection began to fade and MTK members began to realise the potential of NVT.

Science also played a role in changing old habits. As soon as NVT was initiated, the collaborative steering group decided to convene an informal multidisciplinary group of researchers who would potentially be interested in studying the social and

ecological conditions for NVT. The circle of researchers from several universities and research institutes held its first meeting in Pori on 13 June 2003, just one week after the first official collaborative steering group meeting. A large number of researchers were interested in this voluntary arrangement for biodiversity conservation. This habit of convening in Pori once a year continued throughout the pilot.

The motivation for encouraging multidisciplinary research stemmed from the desire to gain a clearer picture of how NVT works in practice and what impact it has. The collaborative steering group primarily worked to achieve institutional goals, i.e., to create and establish the rules and practices of trading. However, the group has had confidence in the positive economic and ecological impacts of NVT. Most of the researchers who accepted the initial challenge to study NVT were social scientists, particularly economists. The composition of the circle is different from that in the Biodiversity Research Programme MOSSE (2002–2006), for instance, in which natural scientists are in the majority. The results were encouraging for the NVT pilot project (Horne et al. 2006, Juutinen et al. 2008, see also Hiedanpää and Bromley 2012, Primmer et al. 2013).

Golden eagle

As noted above, the golden eagle compensation scheme was subsequently revised as the responsibility for compensation was transferred to the Ministry of Environment. Therefore, it was easy to build a new scheme at the administrative level because there were no old organisational habits or structures to be changed.

The greatest organisational change was the increased collaboration among the authorities (the Ministry of the Environment, the Forest and Parks Services, and the Regional Environment Centre in Lapland), volunteer bird watchers, and reindeer owners. This collaboration was formalised with the establishment of the working group in conjunction with the adoption of the scheme. The group follows on-going research on the golden eagle and its effects on reindeer husbandry (Suvantola 2013).

The systematic search for golden eagle nests started as early as 1958, and the Forest and Parks Services have been responsible for the identification and management of golden eagle nests since 1983. Given that the golden eagle compensation scheme adopted in 1999 is based on information about known nesting territories, there was a need for more research and information sharing between the reindeer owners and researchers to ensure the accuracy of the payments. The territories are monitored twice annually: decorated nests (occupied territories) are counted in May, and the offspring are counted in occupied territories in June. Each year, the Forest and Parks Services inform the representatives of each reindeer co-operative about known nests. In turn, the reindeer owners inform the Services representative about potential or suspected nests, which are then monitored by the Forest and Parks Services (Suvantola 2013). Most of the fieldwork is conducted by 30 volunteer bird watchers who have been authorised by the Ministry of the Environment (Below 2000). Thus, the role of the bird watchers was formalised as a result of the adoption of the compensation scheme.

Matching the instrument to local customs and habits

NVT

In NVT, forest owners now had two alternatives: they were compensated for refraining from doing anything or for making an active choice to do something. In the passive approach to natural values production, forest owners simply allow natural values to exist. In the active approach, they may increase the amount of exposed decaying wood, remove species that do not belong to the habit in question, or perform other management or restorative activities to preserve or strengthen natural values. Approximately 40 of the 115 NVT contracts involve active measures by forest owners. Compensation for forest management measures is paid in accordance with the Act on the Financing of Sustainable Forestry.

Hakila and other members of the collaborative steering group were been unanimous in their view of landowners: with respect to the protection of biodiversity, landowners are motivated not by a sense of moral obligation but by the possibility of financial profit. Hakila in particular stressed that individual motives for action are not important in instrument design; what matters is that agreements are reached, that the principles of NVT are more widely adopted, that people learn what the programme is about, and that trading achieves a more established position in the protection of biodiversity. According to Hakila, the sense of moral obligation will follow later of its own accord.

One of the ways in which forest owners' sense of profit were bolstered was by helping them identify natural values in their own forests and determine the price of these values. The collaborative steering group repeatedly emphasised the need to strengthen landowners' commitment to voluntary conservation. Traditionally, nature conservation areas have been kept strictly separate from land designated for forestry use. Hakila, in particular, argued for the need to combine these two categories into a concept of a commercially managed forest in which forestry is practised in such a way that no danger is caused to the typical or unique natural values of the area or, indeed, where those values are reinforced by the practice of forestry. By giving up a small slice of the traditional value added by forestry, it is possible to protect biodiversity and increase economic activity at both the individual and regional levels.

Hakila also attempted to integrate economic history and local activity as part of the protection of biodiversity and sustainable use. Virtually all areas that are significant from a biodiversity perspective, have been objects of human activity and that the safeguarding of biodiversity in these areas requires the continuation of that activity. This was a positive message for farmers in two ways: first, they were no longer accused of impoverishing biodiversity, and second, their active contribution was needed to help resolve the biodiversity problem.

Golden eagle

What makes the golden eagle case especially interesting is that reindeer husbandry is a traditional source of income for the Sami people. The Sami, who are the only indigenous

people in the European Union, are a minority whose language and culture are protected by provisions such as Article 27 of the International Covenant on Civil and Political Rights. This article allows special treatment (positive discrimination) for the Sami to protect their culture and may also be used as a material basis for the protection of their culture. Both forms of protection are safeguarded by the fundamental rights set out in the Finnish Constitution. In addition to the conflict that the recovery of the golden eagle has caused between the conservation of the species and reindeer herding, other environmental conflicts related to the traditional livelihoods of the Sami have arisen. For example, the conflict between state forestry and Sami reindeer herding led to appeals to the UN Human Rights Committee (UNHRC) (Raitio 2008). Although indigenous people are often viewed as ideal nature conservationists, it is important to recognise that not all indigenous lifestyles are necessarily compatible with environmental conservation (Heinämäki 2010). Practices such as hunting and the harvesting of natural resources may conflict with environmental legislation.

According to a survey conducted in 2005, the reindeer owners' attitudes towards nature can mostly be described as utilitarian. Most reindeer owners accept the presence of carnivores in reindeer herding areas, but only if the damages are fully compensated; they also feel that humans have the right to regulate the population of wild animals as they wish (Sippola et al. 2005). Thus, to gain acceptability, a conservation scheme must facilitate the sustainability of reindeer husbandry and be compatible with local customs and habits. Compared to the verified damage compensation scheme, the incentive-based scheme is more successful in this regard, as it makes it unnecessary to look for carcasses, which saves fuel and labour costs associated with verification (Rollins and Briggs 2006). Participation in the scheme does not necessarily require the reindeer owners to conduct any active work. The co-operatives receive compensation each year, regardless of what damage has occurred and regardless of their active participation in the identification and management of golden eagle territories. Naturally, it is in the herders' interest to report the nests they find, as the compensation is greater when more nests are found.

Nevertheless, the scheme did not gain full acceptance immediately. The Supreme Administrative Court in Finland had to review the incentive scheme, as one of the co-operatives made an appeal against the compensation decision in 1999 because the compensation did not cover the confirmed losses of the co-operative. The co-operative consisted mainly of Sami people and argued that the scheme was contrary to Article 27 of the United Nations International Covenant on Civil and Political Rights (1966). That covenant states that in States containing ethnic minorities, for example, persons belonging to such minorities shall not be denied the right, in community with the other members of their group, to enjoy their own culture. The Supreme Administrative Court found in its decision (KHO 12.9.2002 file 2154) that the incentive scheme did not deny the right of the Sami people to enjoy their culture.

Over the years, however, the reindeer owners have learned to trust in the accuracy of the compensation, and the scheme has gained acceptance (Sippola et al.

2005). The role of the research and the trust towards the researchers have been important in this regard. As reindeer owners have become convinced that the compensation rate would increase as new occupied territories were found, but not vice versa (that is, there is no collective punishment for destroyed nests, as the compensations already paid are not required to be paid back), the trust felt by reindeer owners towards the scheme and authorities has increased (Suvantola 2013, Ollila and Ilmonen 2009).

The incentive-based scheme has enabled a shift in reindeer owners' behaviour. Instead of using time and money to find reindeer carcasses and verify damage, they are now able to act for golden eagle conservation because they have incentives to both inform the authorities of nests found and protect their reindeer from damage.

Normalisation of the success

NVT

NVT became standardised with the renewed law on "Financing Sustainable Forestry" (Law on the Financing of Sustainable Forestry 544/2007) in 2008. However, the original parameters have not survived unscathed. The authoritative agents changed some features as the policy innovation was formalised. First, natural values (ecosystem services) are not actually paid for; only the values of timber losses are compensated, according to the list price of €39 per hectare per year. This modification was required because the EU forbids the Finnish government to support forestry in a way that might distort competition with regard to forest-related goods (European Commission C (2008)460/2, Brussels, 13 II 2008.) Second, *all* accepted sites must fulfil the Biological Nature Conservation Criteria (BNCC) (Ministry of the Environment 2003).

The NVT scheme needed to be revised because the EU Commission required the scheme to be consistent with the state aid regulations of the Treaty on the Functioning of the European Union. According to the commission, the forest owners can only be compensated for loss of income (European Commission C (2008)460/2, Brussels, 13 II 2008). Thus, the state cannot offer any compensation that is greater than the loss of income resulting from forgoing timber production, even for sites that would be highly valuable for nature conservation purposes.

In the initial scheme, the price varied according to the ecological significance of the natural values being protected, timber losses, and completed management work, and site selection was contingently stretched outside the criteria of the BNCC. This approach enabled forest owners to suggest the inclusion of areas of lesser importance in the same conservation package as significant areas. However, all contracts must include sites that fulfil the BNCC. In these cases, payments for minor natural values were minimal. In addition, the latitude in price negotiations (+/- 15 per cent) was removed from the formalised NVT. One other change from the original NVT

scheme is that most of the new contracts are permanent rather than for a period of ten years. The new formal policy instrument is now very different from what was successfully implemented in southwestern Finland. In other words, NVT changed as it became formalised. The EU and Finland redefined it to suit their purposes, their authorities, and their competencies. The new product differs from the original general idea. This formalisation process highlights potential institutional barriers to experimenting or learning through experiments, such as inflexible legal norms or their interpretation.

Golden eagle

The golden eagle compensation scheme has been in place since 2000. During this time, the number of known nesting territories has increased from approximately 175 in 1999 to 310–390 in 2012 (<http://www.metsa.fi/sivustot/metsa/fi/Luonnonsuojelu/Lajitjaluontotyypit/Uhanalaisetelaimet/Maakotka/Sivut/Maakotka.aspx> (17.05.2012)). In ecological terms, the scheme can be considered a success. The scheme has also earned the approval of those involved. A survey conducted in 2005 indicated that the reindeer owners were roughly split between those who were fully or mostly satisfied (48 per cent) and those who were not (41 per cent), even though a larger share had a positive view of the scheme (Sippola et al. 2005). However, attitudes changed when the reindeer owners were asked about their willingness to maintain or change the existing incentive scheme. One-fifth of the reindeer owners wanted to maintain the golden eagle incentive scheme as it was, and half wanted to maintain it with some amendments. Only 3 per cent were willing to restore the confirmed damage compensation scheme, and 6 per cent felt that another scheme would be better (Sippola et al. 2005). Therefore, it appears that the overall principle of the incentive scheme has been widely accepted even though the reindeer owners do not consider the design of the scheme to be entirely satisfactory.

Apart from the changes made to the compensation rate, which has increased with the market price for reindeer meat, the scheme has remained almost the same over time. An amendment (amendment 839/2005) was made in 2005 to take unoccupied territories into account if decorated nests or offspring had been found in the previous two years. This amendment was based on the fact that golden eagles may have several nests in a single territory, some of which may not be known, and a pair may change its nesting site from year to year (Suvantola 2013).

According to a representative of the Forest and Parks Services, co-operation between the researchers and reindeer owners has been smooth (Ollila and Ilmonen 2009). To enhance the search for nests, which is largely based on voluntary work conducted by bird watchers, the Forest and Parks Services began to pay awards of €100 for new nests found in the spring of 2012. This procedure was consistent with proposals made by reindeer owners when they were asked how the scheme could be revised. According to the survey, 10.8 per cent of the reindeer owners suggested improved nest surveys and clarification of the size of a territory (Sippola et al. 2005).

Discussion

Having covered some key features and properties of these two PES schemes, the question of why these instruments have succeeded remains. We argue that there are three major elements to the success of these schemes. These elements are institutional entrepreneurship, trust, and crowding-in.

Institutional entrepreneurship

One citizen – Raimo Hakila – was particularly active in NVT. He had the entrepreneurial creativity that the scheme needed. This breed of entrepreneurship is institutional because it led to the renewal of the entire setting of organised and unorganised collective action (Battalina et al. 2009). In the final analysis, it was not just Hakila who made the difference but rather the entire network of collaboration that produced and mobilised different types of capital. In the same vein, the golden eagle case was built on the activism of key people. In this case, however, those entrepreneurial minds did not emerge from the civil society but rather from the realm of legal advisors. The original task was to copy the wolverine compensation scheme used in Swedish Lapland to address the problems with the golden eagle protection scheme used in Finnish Lapland. However, the process was not as simple as copying the Swedish scheme; rather, it entailed institutional design, adjustment, and fine-tuning, of which one civil servant took charge.

A few common features in entrepreneurial activities help explain why they become successful. As a radical invention, NVT promised to change habits of thought and organisational routines that hindered the ability to view protection and production as coexisting, i.e., protection as a mode of production. Because of these changes in thinking and routines, the protection of forest biodiversity no longer meant that the protected areas were permanently excluded from the realm of meaningful use. Instead, as part of NVT, the protected areas came to be seen as part of the economic realm. The incentive not only motivated the forest owners and administrators to act in new ways but also motivated them to think differently, which is one aspect of successful habit change. In other words, the habits of thought (language use) changed, and the concept of *Luonnonarvokauppa* (natural values trading) came to denote all types of voluntary and fixed-time protection and became a metaphor that created opportunities for productive protection. A similar shift in habits occurred in Lapland. Under the new scheme, the presence of the golden eagle is an economic asset, not a nuisance that hinders economic activities. The protection of biodiversity is internalised in the practices of reindeer husbandry.

One could say that the habits of the regulator and the agents changed. The space of possible economic actions was altered, which had long-term effects on forest owners and reindeer herders and on the principals in charge of how these instruments are exercised and developed. Drawing from the legal literature, we can see that the legal

equivalent of the principal – the regulator – does have the final say in terms of how the instruments are designed and implemented. The regulatees faced an NVT that was quite different after the experimental phase written into the Law of Sustainable Financing of Forestry. The habits of mind of the regulatees had, however, already changed in favour of NVT. The strong positive image of its principles was sustained even though the scheme itself was now much tighter than it was in the experimental phase. This type of institutional surprise did not occur with the golden eagle because of the scheme's tight initial design.

Both of our cases indicate that the Schumpeterian creation of a new product, producer, seller, field, and market requires more than simply a shift in language and modes of speaking; it requires motivated action (Schumpeter 1980). In the cases considered here, the conditions of motivation point in a similar direction, namely, towards intensive collaboration between the principals and the agents (stakeholders), i.e., the regulator and the regulatees. This collaboration provided the conditions for experimentation, persuasion, and immediate feedback.

Producing trust

In modern law, the key normative function of the legal system to provide security and stability is achieved ideally through fixed norms and standards. Regulatory instruments based on voluntary action and flexible norms, such as the instruments considered in our case studies, seem to contradict these key legal values (Ruhl 2012). However, as our case studies show, other mechanisms can also be used to provide the stability and security of expectations needed for success. The success of the voluntary instruments builds on the level of confidence in the workability, results, and continuity of these instruments. In our cases, building trust between the regulatees and the regulator has been the key element in this regard. Almost paradoxically, this trust and confidence rest on the trustworthiness of the regulator and the managerial principals. In the case of NVT, not all the regulatees were pleased with the new legal interpretation of NVT in 2008 (Hiedanpää and Bromley 2012).

Trust has been defined in various ways, but a common feature of all the definitions is reciprocity (Fukuyama 1996). For trust to exist, there must be one party that trusts and another party that is trusted. Trust is not only a volitional feature of human interaction; it is also a property of more tacit interrelation and interactions, that is, the interdependence between people and their environments. Together with reciprocity, trust can be characterised by the concept of the security of expectations (Commons 1990).

In our cases, the legislator enabled trust to be built by choosing the use of voluntary instruments. The use of coercive rules and criminal sanctions can deprive people of the experience of being trusted, which destroys the possibility of trust. In that case, legal norms become surrogates for trust. Seen from another perspective, the regulatee must have confidence in the institutional arrangement, broadly understood, that the regulator has initiated and implemented (Sennett 2006). The relation of confidence

is between the regulatees and an institutional arrangement. In both of our cases, the regulatees exhibited confidence in the principles and workability of the schemes, which again helps to explain the success of these schemes.

What is relevant for our case studies is how the sense of being trusted affects individual behaviour and character and identifying the effects in a wider setting of collaboration. Being trusted means being held accountable for the trust of the truster, being held to a standard of behaviour that allows relationships to form and be sustained, and being held responsible by social approbation and feelings of guilt and failure (Mitchell 2001). According to Mitchell, perhaps most importantly, to be trusted is to be considered trustworthy. He also notes that to be told we are trustworthy requires us to behave in a way that reflects that gift (Mitchell 2001). Hakila is widely held to be worthy of trust in the field of forest biodiversity protection in southwestern Finland, and he has actively used this collectively assigned position to expand the positive influence of it. Similarly, in the golden eagle case, trustworthiness is a feature of active and necessary collaboration that constitutes and maintains the workability of the compensation scheme.

The theory of reciprocity suggests the importance of building trust rather than relying on criminal sanctions and coercive regulations, as trust motivates people to act in certain ways (Kahan 2002). This theory is based on social science evidence that individuals in collective action settings do not adopt a materially calculating posture but rather prefer a richer, more emotionally nuanced reciprocal posture. When individuals perceive that others are behaving co-operatively, they tend to be motivated by honour, altruism, and similar dispositions to contribute to the public good, even without the inducement of material incentives or sanctions (Kahan 2002). Individuals thereby help to secure the environment of security of expectations. Trust can motivate people to contribute to the common good because individuals who have faith in the willingness of others to contribute their share will be more likely to voluntarily respond in kind. The logic is that if some individuals conclude that those around them are inclined to contribute, they will respond by contributing in kind, prompting others to contribute, and so on until a highly co-operative state of affairs takes root (Kahan 2002). This process is exactly what we witnessed in our cases.

In addition to creating conditions that enable trust to be built, trust must be sustained. As multi-round public good experiments have shown, communication and interaction are critical elements in producing and sustaining trust (Ostrom 2000). This feature of continued interaction and communication is present in both of our exemplary instruments. A good example of how the lack of communication can lead to distrust and unwillingness to contribute to the conservation is the establishment of the Natura 2000 network in Finland. The distrust between the forest owners and the environmental authorities has had a far-reaching effect on their relationship (Hiedanpää 2002). The NVT scheme has attempted to rebuild that trust.

Communication is also relevant to the question of what binds a trusted person. Although potential harm to reputation and personal loss serve as motivations to maintain trust, those are not expressions of trust as such but rather calculations. According to Ben-Ner and Putterman (2001), these calculations serve as surrogates for the personal

contact that most effectively builds trust. Experiencing, understanding, and accepting the responsibilities that we have as trusted persons is what makes trusting possible without the need for calculation at all. Even if trust begins with calculation, calculation cannot sustain trust. Positive consequences of the exercise of trust produce more trust. Positive consequences of confidence produce more confidence. These processes contribute to a legal and social environment that can be characterised as having higher a security of expectations. Mere rational calculus does not sustain trust. Continuity also involves a moral dimension, which relates to what has been termed “crowding-in”.

Crowding-in

When selecting regulatory instruments to be used, a pragmatic legislator may sacrifice the coherence of the legal system to achieve the best societal outcome. In our case, the best outcome is biodiversity protection. For instance, financial incentive schemes such as NVT and the golden eagle compensation scheme might contradict the legal system, which prohibits the intentional destruction of biodiversity. In other words, why should society pay people to obey the law?

The use of voluntary and economic instruments has been accused of contradicting the polluter-pays principle and moral norms (Oksanen and Kumpula 2008). The argument maintains that individuals do not deserve a reward for complying with legal norms, and if an individual violates the norm, he or she should be punished. When we take a more pragmatic starting point and consider all the information and social context, compensation for damages caused by golden eagles to reindeer husbandry and payment for forest owners to conserve biodiversity on their land are justified.

The question of whether the state has a legal duty to pay compensation for losses caused by wildlife is legally unclear and even debatable, but it is certainly reasonable to cover these losses to avoid more serious harms and conflicts. Refusal to compensate those losses would contribute to the strengthening of the emotional regime in favour of the illegal killing of damage-causing animals (Oksanen and Kumpula 2008). The question of how to compensate for the damages then becomes more important. Compared to the verified damage compensation scheme, the incentive-based scheme has a clear advantage in terms of preventing the moral hazard problem, i.e., a situation in which those suffering the losses receive full compensation and thus have no incentive to carry out damage-abatement measures (Rollins and Briggs 2006).

There is also a concern that economic incentives create an unsuitable attitude towards conservation: the intrinsic value of biodiversity will not be honoured, and biodiversity instead becomes a means to receive income. For instance, payments for ecosystem services have sometimes been shown to have an adverse effect by decreasing the intrinsic motivations to contribute to ecosystem services. This phenomenon, also called “crowding-out”, occurs when internal intrinsic motivations are in conflict with external (economic) incentives (Bowles 2008). For example, the institutional change in blood donation systems based on financial payments reduced the total amount of

blood received. Most donors consider blood donation to be a moral obligation; therefore, a change in the rules of the game eroded the moral grounds of the practice of “giving” blood. Payments corrupted the moral order of blood “donations”. This change could also occur with PES programs (Dedeurwaerdere 2005).

But notice that if the actual payment is not cash but, for instance a health service that is worth money the crowding-out effect does not exist to the same extent (Lacetera et al. 2013). The purpose of blood donation is to support life and health. If the purpose of the donation scheme is the same, then it is considered more acceptable. There is evidence of the emergence of order of the opposite type. The crowding-in effect means that people conform and entrain with a new norm that may also become a new moral standard (Vatn 2005). We could conclude that this change occurred in southwestern Finland with NVT. The key to the crowding-in effect was that the programme enabled new mental habits concerning biodiversity protection as an economic activity. Hence, the PES program unintentionally strengthened the moral commitment to safeguard biodiversity. Landowners, as sellers of natural values, felt it was important for them to have real-life contacts with the buyers as they discussed and agreed upon the terms of the trade (Hiedanpää and Bromley 2012). In the case of the golden eagle, the reindeer owners are concerned about their income and the continuity of their traditional livelihoods. The eagle has become a real and tangible symbol of these concerns. As such, reindeer herders are not primarily motivated by a sense of moral obligation. Paradoxically, then, the crowding-out effect is not likely to become a problem. The same is true for the NVT case: as far as the protection of biodiversity is concerned, landowners are motivated less by a sense of moral obligation than by interests of financial profit. Furthermore, there is evidence that those who would conserve nature for altruistic reasons rather stayed out than entered a contract (Primmer et al. 2014).

Conclusions

The purpose of this paper was to explore why NVT and the protection of the golden eagle can be considered successful biodiversity policies. We have provided a detailed description of the substantive and procedural details of these instruments. We have identified the following reasons for the success of these schemes. First, there was an institutional entrepreneur, that is, an active individual or a group who initiated the key principles of the scheme. Second, this entrepreneur created social incentives for the stakeholders to collaborate in drafting the rules, principles, and practices for the schemes, which in turn, developed agents' confidence in the schemes and trust amongst the agents. Third, due to the collaborative changes in habits of mind and action, the schemes fit with the productive practices and customs of local livelihoods and encouraged the agents and regulatees to voluntarily adjust their behaviour.

This study also highlights the potential institutional barriers that may prevent learning through regulatory experiments and developing governance accordingly. On the one hand, regulatory flexibility and willing regulators are needed for experiments

to take place. On the other hand, adaptability and reflexivity in the legal system are needed to learn from those experiments. As the NVT case clearly indicates, the strict interpretation of EU norms did not allow the scheme to be implemented in its original form, despite its success. Thus, ways to enhance the adaptive capacity (Ruhl 2012, Craig 2010) and reflexivity of the legal system to respond to the changes in social and ecological systems and new knowledge gained may need to be developed.

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Effects of *Dichrostachys cinerea* (L.) Wight & Arn (Fabaceae) on herbaceous species in a semi-arid rangeland in Zimbabwe

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Abstract

Anthropogenic alteration of an environment and other disturbance regimes may enable the expansion of some native species into new geographical areas, a phenomenon observed with *Dichrostachys cinerea*. Five *D. cinerea* invaded sites, each approximately one hectare in size were assessed for the effects of *D. cinerea* on native herbaceous species diversity, richness, basal cover, litter cover, top hamper and plant vigour. The same attributes were studied in five uninvaded sites adjacent to, and equal in size to each invaded site. Forty herbaceous species were identified in the area. There were significant differences ($P < 0.05$) noted in species richness, basal cover, litter cover, top hamper, plant vigour, and species diversities between invaded and uninvaded sites, with uninvaded sites recording higher values than invaded sites. Altitude, erosion and the edaphic variables pH, N, P and K, which were included as explanatory variables, also differed significantly ($P < 0.05$) between invaded and uninvaded sites. Of the 30 *D. cinerea* invaded plots established for herbaceous species assessments, 26 were positively correlated with altitude, erosion, pH, P, N and K. It is imperative to find ways of managing *D. cinerea* in order to reduce its adverse effects on herbaceous species.

Keywords

Dichrostachys cinerea, herbaceous species, invasion

Introduction

Ecologically unsustainable anthropogenic activities such as agriculture, mining, and oil exploration, coupled with climate change and variability, facilitate plant species invasions. This is exacerbated by increases in the frequency and extent of natural disturbances such as droughts, hail storms, fire, insect outbreaks and disease in boreal forests which upset ecological and economic balances, perpetrating invasions (IPCC 2007). The Convention on Biodiversity (CBD) targeted ‘to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional, and national level as a contribution to poverty alleviation, and to the benefit of all life on Earth’ (SCBD 2010). This facilitated development of policies to preserve biodiversity including elimination or control of alien invasive species. Most of the studies on plant species invasion ecology focus on these alien invasives, yet the control of exotic and native species by the same ecological processes may explain the positive correlation often found between exotic and native species richness (Lonsdale 1999).

Dichrostachys cinerea is a deciduous low thorny tree or shrub that produces bicoloured fragrant flowers. It is native to Africa and Asia, where it is common in the tropics of Africa, the Sahelian and Sudanian ecozones, and the South Arabian Peninsula (TTPC 2010). Both old and young *D. cinerea* plants can produce many viable seeds annually which can survive for more than 5 years in the soil. This increases propagule pressure of the species. Its infructescence has a strong aroma, and this probably attracts animals to feed on the pods, facilitating seed dispersal. The species also forms impenetrable thickets that are difficult to eliminate due to high propagation capacity and propagule pressure of *D. cinerea*. Increased grazing and trampling pressure around boreholes was shown to cause a species-poor zone in the immediate vicinity of boreholes, followed by thickets with *Acacia* spp. and *D. cinerea*, transitional to tree savanna (Tolsma et al. 1987a).

Collection and grinding of *D. cinerea* fruits have been suggested as a management tool to control its encroachment (Mlambo et al. 2004). Chemical ways are often costly, and most herbicides are dangerous and have residual effects. Manual control is labour intensive and also less effective since new seedlings and coppicing replace the mechanically removed *D. cinerea* plants. The main aim of this study was to assess the effects of *D. cinerea* on herbaceous species diversity, richness, basal cover, litter cover, plant vigour and top hamper, determining the major herbaceous characteristics of invaded sites and the extent to which invaded and uninvaded sites differ. An analysis of the invasive capacity of *D. cinerea* on rangelands will contribute immensely to its management and control, hence achievement of the 2010 Convention on Biodiversity (CBD) target, which was also incorporated as a new target in the Millennium Development Goals (MDGs).

Materials and methods

Location

Rangelands on Gokomere Farm located 18 km north of Masvingo town, and covering approximately 5800 hectares of land were studied. The farm lies in Natural Region IV (NR IV) of the Zimbabwean ecological classification system (Vincent and Thomas 1961). It is found at an altitude of 1163 m above sea level (19°57'45"S, 30°46'34"E). The farm is characterised by a few small kopjes, semi-vlei areas, and granite outcrops. Its soils are granite derived sandy-loams that are deficient in nitrogen, sulphur and phosphorous. Rainfall is unreliable both within and between seasons. Mean maximum and minimum temperatures of 21.8° C and 13.3° C are often experienced in October and June respectively. *Hyparrhenia* spp. was the main perennial cover, while *Terminalia sericea* and *Combretum* spp. were the main woody species.

Plot demarcation, and herbaceous species and edaphic assessments

A 2009 Google Earth Satellite Imagery of Gokomere Farm, followed by ground truthing was used to identify areas invaded by *D. cinerea*. Five *D. cinerea* patches were chosen using the nearest neighbour-plus-one-method. Three transects measuring 100 m each were laid down, the first one passing through the centre of each patch, and each of the other two at equi-distances from the middle and boundary of each patch. On each transect, two 10 m × 10 m plots were systematically pegged on the ground. They were established at least 50 m from main roads and rivers to reduce road and river effects. Species presence/absence data and other herbaceous assessments were carried out in five 1 m × 1 m quadrats established at the four corners and centre of each 10 m × 10 m plot (Mueller-Dombois and Ellenberg 1974). For each quadrat, herbaceous cover, litter cover, top hamper, erosion and plant vigour were awarded numeric values ranging from 1-10 whereby the higher the attribute, the higher the value. Altitude and location of the sites were recorded using a Geographical Positioning System (GPS) unit. A soil auger was used to collect soil from the top 15 cm of the soil from each of the quadrats (Stohlgren et al. 1998). The soil samples from the same plot were thoroughly mixed and the composite sample was put in an air proof polythene bag. Analysis was done on N, P, K and pH at the Department of Soil Science, University of Zimbabwe.

Data analysis

SPSS Version 13.0 (2004) was used for one way analyses of variance (ANOVA) of the herbaceous and soil variables. PAST was used to calculate diversity indices. The herbaceous variables that were analysed were basal cover, litter cover, plant vigour and top

hamper. Altitude, erosion and the edaphic variables (pH, N, P and K) were included as explanatory variables. Multiple comparisons were done to test for significant differences among the plots. The relationships between the measured variables and the measured explanatory variables were explored using CANOCO for Windows (version 4). CANOCO was used to carry out Detrended Correspondence Analysis (DCA) and Redundancy Analysis (RCA) (ter Braak and Smilauer 1998). RCA was used to detect relationships using species data and the environmental variables measured. An unrestricted Monte-Carlo permutation test in CANOCO was used to test the statistical significance of the ordination (CANOCO, version 4.5 2002).

Results

Herbaceous variables

There was a total of 40 herbaceous species in the *D. cinerea* invaded and uninvaded sites. Invaded sites had 26 species while uninvaded sites had 32. The most common species in the invaded sites were *Digitaria penzii*, *Cynodon dactylon* and *Eragrostis trichophora* while in the uninvaded sites they were *D. penzii*, *E. trichophora* and *Hyperthelia dissoluta* (Table 1).

There were significant differences ($F_{9,50}=9.375$, $P<0.05$) in basal cover among invaded and uninvaded sites. Invaded sites did not differ significantly ($F_{9,50}=2.750$, $P>0.05$) in basal cover among themselves. However, the uninvaded sites showed significant differences ($F_{9,50}=16.123$, $P<0.05$). Litter cover had significant differences among invaded and uninvaded sites ($F_{9,50}=6.024$; $P<0.05$). Invaded sites were significantly different from each other ($F_{9,50}=3.442$, $P<0.05$), as were the uninvaded sites ($F_{9,50}=6.537$, $P<0.05$). Invaded sites recorded lower litter cover than uninvaded sites. Plant vigour in invaded sites was significantly different from that within uninvaded sites ($F_{9,50}=5.796$, $P<0.05$). Both the invaded sites and uninvaded sites showed significant differences in plant vigour ($F_{9,50}=8.037$, $P<0.05$ and $F_{9,50}=4.605$, $P<0.05$ respectively) among themselves. There were significant differences in top hamper among invaded and uninvaded sites

Table 1. Herbaceous species variables among the invaded and uninvaded sites.

| Parameter | Invaded Site | Uninvaded Site |
|-------------------|-------------------|-------------------|
| Basal cover | 3.7 ^a | 4.5 ^b |
| Litter cover | 1.5 ^a | 2.1 ^b |
| Species richness | 2.9 ^a | 3.5 ^b |
| Plant vigour | 2.9 ^a | 3.4 ^b |
| Top hamper | 0.8 ^a | 1.1 ^b |
| Shannon_H index | 2.58 ^a | 2.85 ^b |
| Simpson_1-D index | 0.92 ^a | 0.94 ^b |

Means in rows with different superscripts are significantly different ($P<0.05$)

($F_{9,50}=3.264$, $P<0.05$). Invaded sites did not differ significantly ($F_{9,50}=0.666$, $P>0.05$) in top hamper. Uninvaded sites had significant differences ($F_{9,50}=6.959$, $P<0.05$). Species richness differed significantly ($F_{9,50}=5.776$, $P<0.05$) among invaded and uninvaded sites. Invaded sites were not significantly different ($F_{9,50}=1.052$, $P>0.05$) from each other in species richness. However, uninvaded sites had significant differences ($F_{9,50}=7.113$, $P<0.05$). Herbaceous species diversities also differed significantly ($P<0.05$) between invaded and uninvaded sites.

Edaphic properties

The pH values across invaded and uninvaded sites were significantly different ($F_{9,50}=2.816$, $P<0.05$). Invaded sites had significant differences for pH among themselves ($F_{9,50}=4.738$, $P<0.05$) unlike uninvaded sites ($F_{9,50}=1.719$, $P>0.05$). There were significant differences ($F_{9,50}=70.903$, $P<0.05$) for K between invaded and uninvaded sites. Both, invaded and uninvaded sites were significantly different from each other ($F_{9,50}=100.952$, $P<0.05$; $F_{9,50}=4.535$, $P<0.05$). The recorded P values showed significant differences ($F_{9,50}=66.916$, $P<0.05$) between invaded and uninvaded values. Both invaded and uninvaded sites showed significant differences among themselves ($F_{9,50}=51.018$, $P<0.05$ and $F_{9,50}=24.872$, $P<0.05$ respectively). There were significant differences ($F_{9,50}=3.980$, $P<0.05$) for the recorded N values between the invaded and uninvaded sites. Uninvaded sites significantly differed from each other ($F_{9,50}=5.039$, $P<0.05$) while invaded sites were not significantly different ($F_{9,50}=2.735$, $P>0.05$). There were significant differences ($F_{9,50}=6.193$, $P<0.05$) in altitude between the invaded and uninvaded sites. Invaded sites were significantly different ($F_{9,50}=5.692$, $P<0.05$) from each other. Uninvaded sites also significantly differed ($F_{9,50}=7.637$, $P<0.05$) from each other. Erosion significantly differed ($F_{9,50}=3.303$, $P<0.05$) between invaded and uninvaded sites. Invaded sites had significant differences for erosion among themselves ($F_{9,50}=4.420$, $P<0.05$), and so did uninvaded sites ($F_{9,50}=3.182$, $P<0.05$).

Herbaceous species-environmental relationships

Of the 30 *D. cinerea* invaded plots (1–30) assessed for herbaceous species attributes, 26 were correlated with altitude, erosion, pH, P, N and K (Figure 1). Twenty five of the uninvaded plots (31–60), were negatively correlated with the measured environment variables. Invaded plots classified with these uninvaded sites were 6, 22, 23 and 25. They had low K values characteristic of the uninvaded sites studied, with the exception of sites 4 and 6. They all had lower N than the invaded plots (0.5–2.1 ppm compared to 3.3–5 ppm). There was no clear pattern for pH.

The species that were negatively correlated with these variables were *Aristida* spp., *Pogonathria squarrosa*, *Rhynchelytrum repens*, *Panicum* spp. and *Digitaria penzii*. K was positively correlated with *Urochloa mozambicensis*, *Heteropogon contortus*, *Acanthosper-*

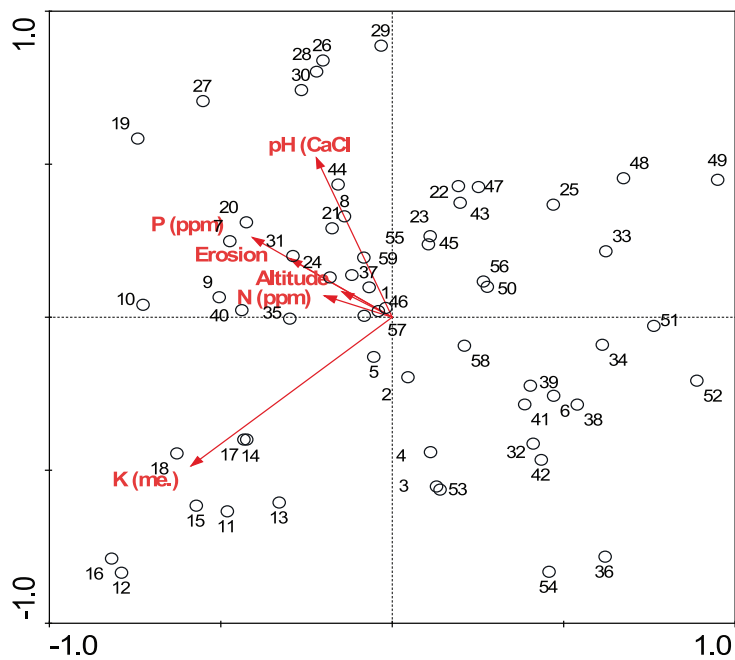


Figure 1. A redundancy analysis plot based on herbaceous species presence absence data showing relationship between the environmental variables and the plots.

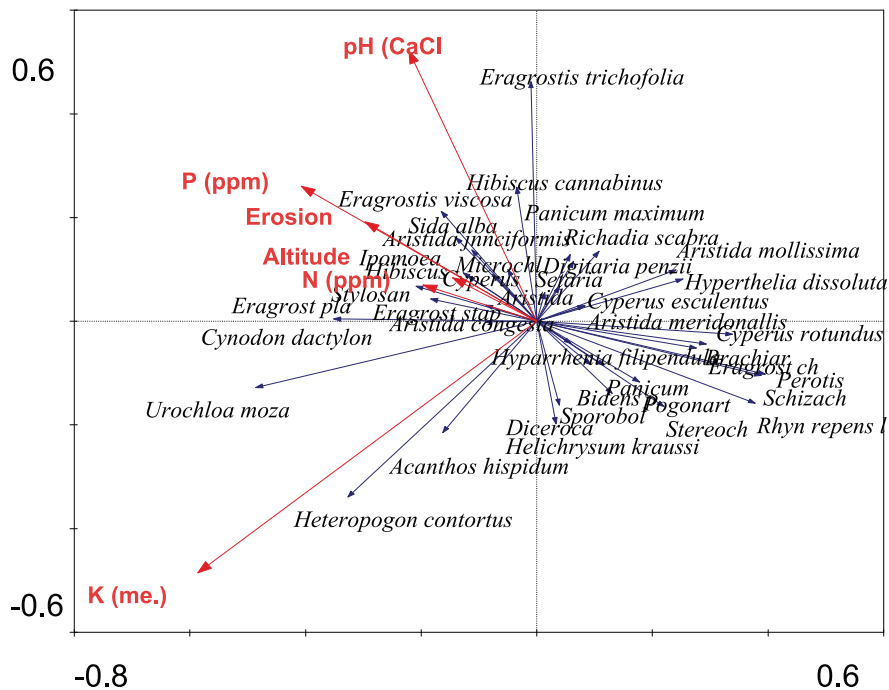


Figure 2. A redundancy analysis plot based on herbaceous species presence absence data showing relationship between the environmental variables and the species.

mum hispidum etc. It was negatively correlated with *Richardia scabra*, *Setaria palidifusca* and *Hyperthelia dissoluta* (Fig. 2).

We show that pH, erosion, P, altitude and N influenced the abundance of species such as *Hibiscus* spp, *Sida alba* and *Cynodon dactylon*.

Discussion

Herbaceous variables

D. cinerea invasion has caused declines in herbaceous species richness. Competitive interactions are critical between woody plants and grass dominated layers in arid to semi-arid areas (Jacoby et al. 1982). *D. cinerea* may be competing with the native herbaceous species for resources such as light, nutrient and moisture. *C. dactylon* was one of the most abundant herbaceous species. It is very competitive, particularly in fertile soils, and only aggressive legumes are capable of forming an association with it (Harlan and de Wet 1969). This explains its occurrence in invaded sites. High litter deposition by a dominant plant species can also modify competition; suppress competing plants, and lower plant species richness (Xiong and Nilsson 1999). *D. cinerea* may have reduced herbaceous species richness through litter deposition or due to its vigorous growth characteristic, extensive and dense root system that is important in propagation and recruitment as compared to native species. Uninvaded sites also recorded higher species diversity indices (Shannon Weiner and Simpson's indices) than the invaded sites. Due to occurrence of certain species only unique to uninvaded sites in the absence of the suppressive nature of *D. cinerea* on other species, uninvaded sites had higher species richness than the invaded sites, hence higher Shannon-Weiner index.

In a study by Tolsma et al. (1987b), there was less than 10 % ground cover by herbs and grasses in *D. cinerea* thickets, with the most frequent species being annual herbs like *Boerhavia diffusa* and weedy species such as *A. hispidum*, the latter of which was only found in invaded sites in the present study. Dense thickets such as those that are formed by *D. cinerea* can result in a decrease in carrying capacity through loss of grass cover caused by replacement and by competition for limited resources. In studying an invasive species of the genus *Prosopis*, although there were certain grasses that were adapted to shade conditions, there were others which were shade intolerant and were thus inhibited by competition with species of genus *Prosopis* (Jacoby et al. 1982). *P. maximum* grows better at 30 % shade although yields are reduced by half at 50% shade (Harty et al. 1983). In the present study *P. maximum* was found in uninvaded sites which had lower canopy cover than the *D. cinerea* invaded sites, hence less shading. The reduced abundance of herbaceous species in this study could also be due to the negative impacts of increased *D. cinerea* canopy cover which may affect shade-intolerant species. Light deprivation may have affected basal cover, plant vigour and richness of herbaceous species noted in invaded sites as compared to uninvaded sites. The occurrence of *H. contortus* under the dense *D. cinerea* thickets is also in consistency with findings that *H. contortus* tolerate light shading, often dominating the understo-

rey of *Eucalyptus* woodlands in tropical and subtropical Australia (Bhatt et al. 2006). While standing litter may protect seedlings from desiccation and high temperatures, it may also reduce light availability (Kaller 2003) hence affect growth and production of other herbaceous species resulting in the observed lower herbaceous basal cover of invaded sites than that of uninvaded sites. Rapid root suckering of *D. cinerea* in propagation as well as high seed germination also make the specie a more successful invader with better plant vigour than the native herbaceous species.

In the present study there were significant differences in environmental variables between invaded and uninvaded sites. Invaded sites had higher soil N, K and P than uninvaded sites. Biological invaders change ecosystems as they differ from native species in resource acquisition and/or resource use efficiency. They may also alter the trophic structure of the area invaded, or the disturbance frequency and/or intensity (Vitousek 1990). The fluctuating resource availability theory states that plant species invasions are associated with increases in resources (Davis et al. 2000). *D. cinerea* is a nitrogen fixing shrub. The effect it has on soil could have been translated into herbaceous species composition. The decline in species richness means that native species are displaced by *D. cinerea*, resulting in a decrease in nutrient sequestration, hence increases in N, P and K observed in the invaded sites. Altitude also varied significantly among invaded sites. *D. cinerea* can occur on a wide range of altitude.

Eragrostis spp., *Hibiscus* spp., *S. alba* and *U. mozambicensis* were found in the *D. cinerea* invaded sites. These grasses are associated with disturbed land (Wild 1972). Disturbance is one of the major factors affecting species invasions (Davis et al. 2000). The *Eragrostis* spp. were positively correlated with erosion and negatively correlated with K. *E. viscosa* is an indicator of poor soil conditions such as is characteristic of eroded land (Wild 1972). *E. chapelierii* is also common on sandveld and it has poor forage value. Eroded soils are low in soil nutrients such as N, P and K. Erosion mostly affects the topsoil which provides the main nutrients needed by plants. *U. mozambicensis* is usually found in wooded grassland and deciduous bushland, or on disturbed sites where the soil is fertile (Burt et al. 1980). This explains the positive correlation of the species with potassium in *D. cinerea* invaded sites. *Stylosanthes guianensis* can extract P very efficiently from low P soils, but still responds to applications of P, as well as K, sulphur and calcium in soils with low levels of these nutrients (Chakraborty 2004). The species was positively correlated with K. *C. dactylon* was one of the most abundant herbaceous species. It grows on a wide range of soils, but best in relatively fertile, well-drained soils. It was correlated with N. It is very competitive, particularly in fertile soils.

The herbaceous species that were negatively correlated with the measured environmental variables were *Aristida* spp., *P. maximum*, *Pogonarthria squarrosa*, *D. penzii*, *H. filipendula*, *H. dissoluta* and *R. repens* among other species. *P. maximum* grows best in moist, well-drained soils just like *R. repens*, although some of its varieties are tolerant of lower fertility and poorer drainage (Harty et al. 1983, Wild 1972). The species was found in uninvaded sites which had lower canopy cover than the *D. cinerea* invaded sites, hence less shading. The correlation of *P. squarrosa* with uninvaded sites is in

consistency with the findings of Wild (1972) who report that the species is a normal constituent of grassland on sandy soils. The *Aristida* spp. are drought resistant perennial grasses that grow in poor, gravelly soils and also on clay soils.

Conclusion

Dichrostachys cinerea is a native invasive woody shrub or tree. Here, it adversely affected native herbaceous species plant vigour, basal cover and species richness. Reduced litter cover and top hamper were also observed in invaded sites. These observations can be attributed to the fast growth, propagation and propagule pressure that characterize *D. cinerea*, giving it a competitive advantage with respect to acquisition of light, nutrients and other resources. Therefore, these adverse effects on herbaceous species may, in the long term, reduce the carrying capacity of rangelands, making them even more susceptible to alien invaders. However, a long-term study may provide more information on the biology and invasive capacity of the species and on its impact on other vegetation and animal species. There is also need to find environmentally friendly and effective methods of controlling *D. cinerea* in order to prevent its spread, hence adverse effects on herbaceous species.

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