RESEARCH ARTICLE

Relating tradable credits for biodiversity to sustainability criteria in a dynamic landscape

**Douglas J. Bruggeman · Michael L. Jones ·
Kim Scribner · Frank Lupi**

Abstract Tradable biodiversity credit systems provide flexible means to resolve conflicts between development and conservation land-use options for habitats occupied by threatened or endangered species. We describe an approach to incorporate the influence of habitat fragmentation into the conservation value of tradable credits. Habitat fragmentation decreases gene flow, increases rates of genetic drift and inbreeding, and increases probabilities of patch extinction. Importantly, tradable credit systems will change the level of fragmentation over time for small and/or declining populations. We apply landscape equivalency analysis (LEA), a generalizable, landscape-scale accounting system that assigns conservation value to habitat patches based on patch contributions to abundance and genetic variance at landscape scales. By evaluating habitat trades using two models that vary the relationship between dispersal behaviors and landscape patterns, we show that LEA provides a novel method for limiting access to habitat at the landscape-scale,

recognizing that the appropriate amount of migration needed to supplement patch recruitment and to offset drift and inbreeding will vary as landscape pattern changes over time. We also found that decisions based on probabilities of persistence alone would ignore changes in migration, genetic drift, and patch extinction that result from habitat trades. The general principle of LEA is that habitat patches traded should make at least equivalent contributions to rates of recruitment and migration estimated at a landscape scale. Traditional approaches for assessing the "take" and "jeopardy" standards under the Endangered Species Act based on changes in abundance and probability of persistence may be inadequate to prevent trades that increase fragmentation.

Keywords Tradable credits · Endangered
Species Act · Habitat fragmentation · Extinction risk ·
Landscape genetics · Landscape equivalency
analysis · Ecosystem services · Red cockaded
woodpeckers · Gene flow · Genetic drift

D. J. Bruggeman (✉) · M. L. Jones
Department of Fisheries and Wildlife, Michigan State
University, East Lansing, MI 48824, USA
e-mail: bruggem3@msu.edu

K. Scribner
Department of Zoology, Michigan State University, East
Lansing, MI 48824, USA

F. Lupi
Department of Agricultural Economics, Michigan State
University, East Lansing, MI 48824, USA

Introduction

Land use change is predicted to be the biggest threat to biodiversity in the coming century (Sala et al. 2000). General principles to predict changes in species occurrence due to land use change remain elusive (Fahrig 2003). Empirical evidence indicates that both species- and landscape-specific attributes are

important (MacNally et al. 2000; Lindenmayer et al. 2008), which may be indicative of the influence landscape history, or the timing of land use change, has on species occurrence (Schrott et al. 2005). The study of effects of land use change on biodiversity has been dominated by literature evaluating the effects of habitat loss and fragmentation (Haila 2002). This work has generated much debate regarding the relative influence on species occurrence of the loss of habitat area versus the breaking apart, or fragmentation, of habitat (Fahrig 2003; Lindenmayer and Fischer 2007). The debate results from the inability of most studies to separate the effects of habitat loss versus fragmentation on biological mechanisms (Fahrig 2003; Lindenmayer and Fischer 2007). For example, loss of habitat area will have a direct effect on rates of recruitment while an increase in degree of fragmentation will have a direct effect on rates of migration. There is also potential for indirect effects, such as the dependence of migration rates on rates of recruitment (Bruggeman and Jones 2008). Identifying which biological mechanisms have been altered by which component of land use change is a critical step in devising mitigation strategies (Lindenmayer and Fischer 2007).

Methods are needed to devise the appropriate mix of increased habitat area and connectivity for species threatened by land use change. However, these mitigation strategies must recognize the political realities of decision making. Economic incentives for biodiversity (e.g., tradable credit systems; Bayon 2002) represent politically realistic approaches for mitigating the effects of land use change. Tradable credit systems such as conservation banking for endangered species in the U.S. (USFWS 2003a) require practitioners to offset the loss of specific habitat patches with the protection or restoration of habitat elsewhere within the landscape. The fundamental issue is the ecological equivalency of habitats traded. Habitat patches traded must make equivalent contributions to rates of recruitment and migration to prevent trades from reducing population viability at a landscape scale (Bruggeman et al. 2005).

Tradable credit systems rely heavily on the application of sustainability criteria to ration access to public goods and services (Tietenberg 2004). Tietenberg (2004) outlines two critical steps for setting up a tradable credit system: 1) setting a limit on user access to resource (e.g., Total Allowable Catch in fisheries and Total Emissions Allowed for air quality), and 2) allocating access rights to resource users as long as limits are not violated. The ESA functions to set limits on user access to habitat by requiring that a "take" (harming, harassing, or killing individuals) be mitigated to the maximum extent possible while not jeopardizing species' survival and recovery (Stanford Environmnental Law Society 2001).

We question whether typical application of these "take" and "jeopardy" standards have utilized adequate measures of ecological quality to ensure equivalent habitats are traded, especially for spatially subdivided populations. Subdivided populations often require migration and variance in rates of recruitment among population units to be persistent at a landscape-scale (Hanski and Gaggiotti 2004). If one evaluates a "take standard" based on changes in abundance (Fox and Nino-Murcia 2005), then even if habitat patches traded are occupied in equal abundance, populations inhabiting these patches may differ in recruitment, survival, or in their ability to facilitate the exchange of individuals across the landscape (Van Horne 1983; Pulliam 1988). Thus, in addition to abundance, many other factors that contribute to regional population sustainability should be evaluated.

Population viability analysis (PVA) is the recommended approach for determining if habitat trades violate the "jeopardy standard" (USFWS 2003a). Demographic parameters can be incorporated into PVA assessment to estimate probabilities of extinction under alternative management scenarios (Brook et al. 2000). Individual-based, spatially-explicit population models (IB-SEPMs) are often used in PVA to predict the effects of habitat loss and fragmentation because they explicitly simulate interactions between a species' life history traits and physical attributes of landscapes and how these attributes change over time (Grimm et al. 2005). Bruggeman and Jones (2008) recommended using IB-SEPMs to determine if habitat patches traded make equivalent contributions to minimizing extinction risk. Importantly, findings indicated that even if no change in probability of total population extinction results from a trade, rates of local extinction within a landscape may change for habitat patches that are not involved in trading.

Landscape change can have multiple effects on populations (Haila 2002). For example under habitat trading policies, rates of recruitment and migration will change concurrently as habitat area and

connectivity changes over time. Therefore, Bruggeman et al. (2005) proposed the integration of economic and population genetic theory to determine the appropriate limit on access to habitat at a landscape-scale. Population genetic studies have shown that spatially subdivided populations benefit from migration rates that are high enough to episodically contribute to recruitment, thereby lowering rates of loss of genetic diversity and rates of inbreeding accrual, but low enough to maintain genetic differences among breeding groups to provide opportunities for adaptive evolution (Mills and Allendorf 1996; Wang 2004). However, the appropriate amount of migration required to offset genetic drift and inbreeding will vary based on an organism's natural history and the degree of habitat loss and fragmentation at the landscape level (Lindenmayer and Lacy 1995; Daniels et al. 2000).

We devised Landscape Equivalency Analysis (LEA) as a method for ensuring that rates of recruitment and migration across the landscape, at a minimum, do not decrease after habitat patches are traded (Bruggeman et al. 2005). This is accomplished under the ESA by supplementing take and jeopardy standards that were traditionally evaluated based on expected changes in abundance and extinction risk, with expected changes in average genetic variance within and among breeding groups (Nei 1973). Conservation value is then determined by comparing predicted temporal changes in abundance and genetic variance expected with and without mitigation with a "baseline" landscape, which represents a spatial apportionment of habitat that minimizes inbreeding, genetic drift, and local extinction, while minimizing loss of genetic variance within and accrual between patches. Habitat trades that lead to rates of recruitment and migration that more closely reflect levels observed in a baseline landscape, can potentially increase the number of tradable credits available.

The objective of this paper is to provide an example of how LEA can be integrated with an IB-SEPM to reflect changes in migration, genetic drift, and local extinction that result from trades for a species of conservation concern. First, we provide a brief overview of LEA (Bruggeman et al. 2005) and describe two habitat trading scenarios. Then we briefly describe an IB-SEPM for the Red-cockaded Woodpecker (RCW, *Picoides borealis*), which we use as a case-study species. Results from LEA are

contrasted with estimates for probability of persistence, which is more commonly used. Importantly, we show that the integration of population genetic and natural resource economic theory provided by LEA yields a more thorough assessment of patch conservation value than is possible through estimates of probability of persistence alone.

Methods

Landscape equivalency analysis

LEA is an extension of resource-based compensation applied to a landscape-scale. Resource-based compensation determines the amount of restoration required to equate an individual's well-being before loss of an ecological resource with their well-being after that loss (Jones and Pease 1997). A "service-to-service" approach is used wherein adequate compensation is made to the public if the habitats restored provide equivalent types and levels of ecological services as the habitats lost. Ecological functions can be treated as goods and services when a direct or indirect benefit to humans can be demonstrated (deGroot et al. 2002). In this analysis we assume that the ecological services that provide these benefits are abundance and genetic variance (Loomis and White 1996; Bruggeman et al. 2005). LEA estimates the equivalency of habitat patches traded in a fragmented landscape based on changes in three ecological services, (1) abundance and genetic variance (2) within and (3) among local populations, measured at the landscape-scale.

The spatial apportionment of neutral genetic variance is included to ensure that trades do not move the *balance* between genetic drift, local extinction, and migration farther away from that observed under a "baseline" landscape. Neutral genetic variance is the variety of alleles present in the population that do not contribute to adaptive traits and whose fate is determined by genetic drift, gene flow, inbreeding, and local extinction (Manel et al. 2003). These effects are the dominant evolutionary forces for small and declining populations (Spielman et al. 2004). Spatially subdivided populations in intact landscapes have demonstrated an ability to maintain genetic variance both within and among breeding groups while preventing inbreeding depression (reviewed in

Bruggeman et al. 2005). The baseline landscape represents the spatial distribution of habitat in which rates of recruitment and migration achieve this balance. Therefore, LEA incorporates a "spatially-explicit" planning objective as the allocation of habitat yielding the spatial apportionment of neutral genetic variance observed prior to habitat loss and fragmentation (i.e., a baseline landscape) (Meffe 1996; Bruggeman et al. 2005). In this way, LEA focuses on protecting the environmental context that permitted adaptive evolution, rather than attempting to identify all adaptive components of genetic variance (Moritz 2002). We follow the habitat equivalency literature in our use of the term "baseline", but note that in restoration ecology this would be referred to as the "reference landscape" (Bell et al. 1997).

Applying LEA to RCWs

Application of LEA requires comparing ecosystem services in different landscapes to estimate the change in services due to habitat trading. First, we project services over time assuming no policy intervention occurs to change landscape structure (i.e., a status quo landscape). The status quo landscape was constructed to represent a highly fragmented distribution of longleaf pine savannah, which represents RCW breeding and foraging habitat. The resulting distribution of habitat (Fig. 1a) is typical of landscapes the USFWS must consider when private landowners make a request for an incidental take (William McDearman and Ralph Costa, USFWS, personal communication). The cell size on the grid, 50 ha, was based on the average RCW territory size observed in high quality RCW habitat, 47 ha (Engstrom and Sanders 1997), which corresponds to the local scale for biological processes (e.g., recruitment). We used 50 × 50 grids comprising a total of 125,000 ha.

The status quo landscape was generated using fractal Brownian motion (Hastings and Sugihara 1993), assuming a fractal similarity value of 0.5 to simulate the random distribution of three land cover types. We specified that RCW habitat cover approximately 2–3% of the landscape to simulate observed densities (Frost 1993), which resulted in a landscape containing 50 RCW territories. The remaining other two land cover types were roughly evenly distributed between non-forested areas and pine-hardwood mixed forests. Non-forested areas were included because it

has been observed that RCWs avoid crossing non-forested areas during movement (Conner and Rudolph 1991). Pine-hardwood mixed forests were included because successional or other man-made actions can be applied to this cover type to re-establish RCW habitat (Walters et al. 2002), which will be useful later when we simulate the addition of a conservation bank.

Next, we constructed a baseline landscape (Fig. 1b) to represent one of the many possible clumped distributions of 50 territories to meet the Private Lands Conservation goal for RCWs (USFWS 2003b). By contrasting expected changes in population structure in the status quo to this baseline landscape we can estimate the effects of fragmentation independent of habitat loss.

To simulate habitat trading, other landscapes were created by adding or removing habitat from the status quo landscape at different times. We only considered one mitigation landscape. The importance of a clumped distribution of habitat is well known for RCWs (USFWS 2003b), so we did not consider alternative placements of a mitigation bank. We assumed that pine-hardwood mixed forests can be restored to provide RCW habitat to create a conservation bank. To generate the mitigation landscape (Fig. 1c), 12 restored territories were added to the center of the status quo landscape at year 20.

Two different withdrawal landscapes were considered by simulating the loss of habitat (take or withdrawal) that differed in levels of structural connectivity. We estimated the structural connectivity of each territory, as recommended by the RCW Recovery Plan (USFWS 2003b), as the number of territories within 3.5 km. In the first scenario, Withdrawal 1 (w1; Fig. 1d), 12 territories with the greatest connectivity values (i.e., 4 or 5 territories within 3.5 km) among RCW territories were cleared for development in year 25. In Withdrawal 2 (w2; Fig 1e), 24 territories with the lowest connectivity values (0, 1, 2, or 3 nearby territories) were cleared for development, also in year 25. Withdrawal 2 then contrasts Withdrawal 1 by removing twice as much habitat area but the habitats lost had lower values of structural connectivity than habitats restored as a bank. Therefore, if we find that Withdrawal 2 is a viable trade, then habitat connectivity can be substituted for losses in habitat area. In contrast, Withdrawal 1 represents an equal trade for both habitat area and connectivity.
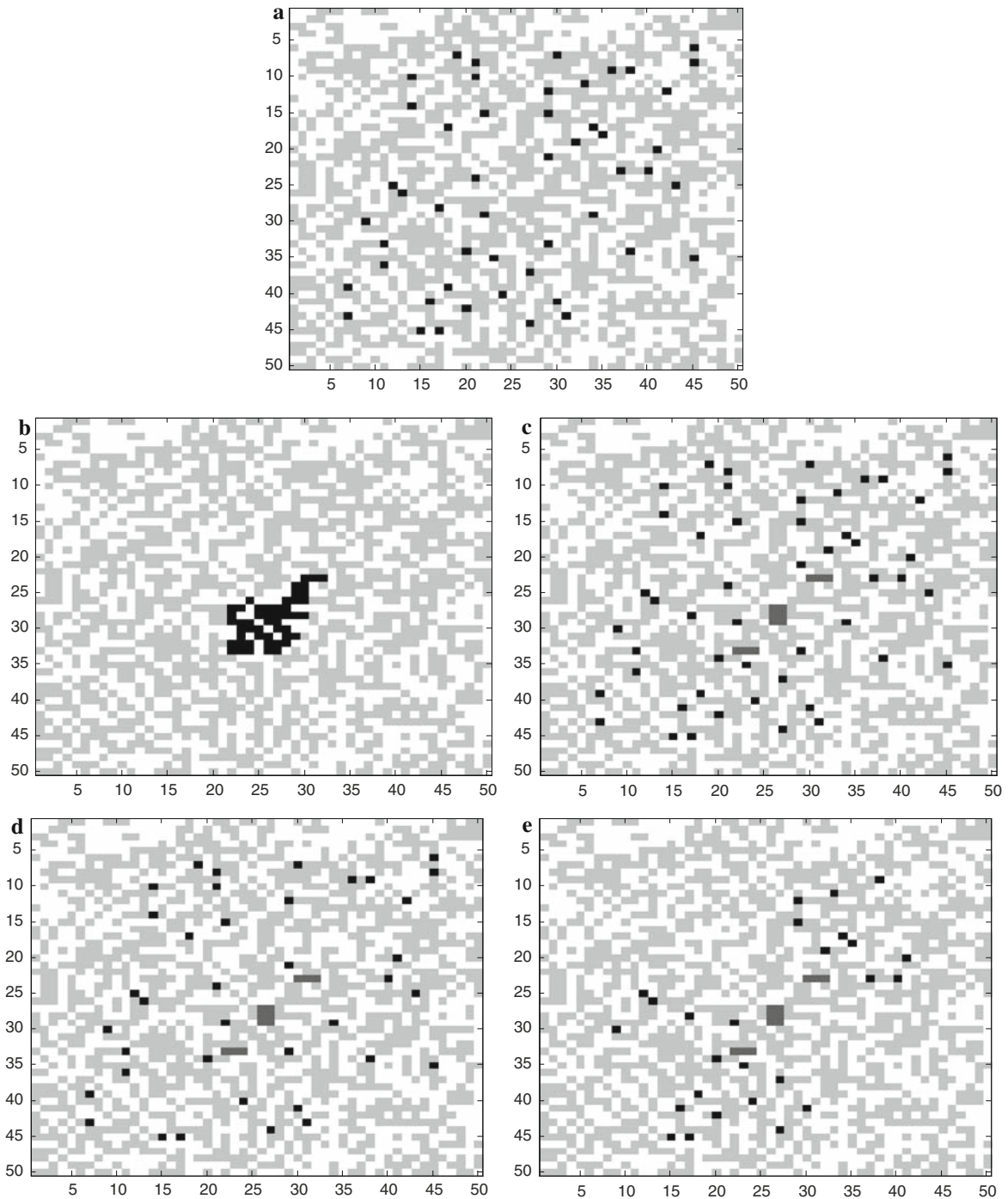
Fig. 1 Stylized landscapes used in simulation study. Each cell represents 50 ha. RCW habitat, longleaf pine savannah (*black cells*), mixed pine-hardwood forest (*light grey cells*), and non-forested (*white cells*). As an initial condition each RCW habitat cell contained one RCW breeding group. **a** Fragmented or status quo landscape requiring management to achieve population persistence **b** Baseline landscape with 50 territories clustered to achieve persistence (USFWS 2003b). **c** Mitigation landscape with 12 cells in the center restored as RCW habitat (*s*). **d** Withdrawal 1 landscape, wherein 12 cells that were well connected to the initial RCW habitat were lost to development. **e** Withdrawal 2 landscape, wherein 24 cells that were poorly connected to the initial RCW habitat were lost to development

RCW IB-SEPM

The RCW IB-SEPM has been described in detail elsewhere (Letcher et al. 1998; Bruggeman and Jones 2008). Therefore, we provide here only a brief description summarizing the hierarchical organization of the model.

Individual behavior

RCWs are a cooperative breeding species in which family groups consist of a reproductively active male and female, nestlings or fledglings, and, occasionally, helpers who are usually male and full or half-sibs to the fledglings (Walters et al. 1988). As an initial condition, we assumed that all RCW habitat cells in our landscape start with a breeding pair. The average number of helpers observed in high quality RCW habitat, based on two years of observations, were 1 and 1.6 helpers per territory (Engstrom and Sanders 1997). We randomly selected half of the territories for the addition of 2 helpers. Floaters are also included in the model, both male and female, which move continuously seeking a breeding vacancy in a territory. Following the Letcher et al. (1998) model we assumed that all fledglings, helpers, floaters, and solitary males can compete for breeding vacancies within 3.5 km of their current location.

Good instruments of policy need to be able to consider the influence of key uncertainties regarding the system being managed. Here, as in Bruggeman and Jones (2008), we illustrate this by evaluating the sensitivity of LEA credits to alternative behavioral assumptions regarding RCW dispersal. We compared two dispersal models. The first was a "random-straight" model, in which the probability of fledgling males delaying dispersal, and remaining as helpers, is constant, birds choose their initial direction of travel at random, and birds travel in a straight line (Letcher et al. 1998). The second dispersal model assumed that landscape cover types affect initial direction of travel, probability of male natal dispersal, and directional choices during movement. To simulate the influence of landscape structure on directional choices after the initial step we assigned four levels of preference during movement to the eight cells adjacent to the bird's current location (Bruggeman and Jones 2008). We assumed that the initial RCW habitat cells were twice as attractive as the restored RCW habitat, restored RCW habitat was 2.5 times as attractive as pine-hardwood mixed forest, and pine-hardwood mixed forest was 4 times as attractive as non-forested areas. In general, these two alternative models represent fundamentally different hypotheses about how RCW use or do not use landscape pattern to influence their movement behaviors.

Genetic variance

To examine how the processes of genetic drift, gene flow, and inbreeding interact in a spatially subdivided population as landscape structure changes, an infinite alleles model of genetic variance was used (e.g., Miller and Lacy 2005). We assigned two unique alleles to one locus for each breeder at the start of the simulation (i.e., total alleles = 2 x number of breeders in the founding population). Assuming Mendelian inheritance, offspring had an equal probability of inheriting each of two alleles.

The expected apportionment of genetic variance within and among breeding groups was estimated by the method of Nei (1973). Total genetic diversity in the population (H_T) was apportioned into components including the average genetic diversity within breeding groups (H_S) and average genetic divergence among breeding groups (D_{ST}), $H_T = H_S + D_{ST}$. Nei defines total genetic diversity (H_T) as the probability that any two alleles chosen at random are independent. Average gene diversity within breeding groups (H_S) equals the probability that two alleles chosen at random from within an individual are independent, averaged across the breeding groups. D_{ST} represents the probability that two genes are different when chosen at random from individuals in two different breeding groups (i.e., habitat patches) averaged across the entire population. This method uses allele frequencies of the current population avoiding unrealistic assumptions regarding random uniting of gametes, rates of drift within groups, or patterns of migration among groups (Nei 1986), making it useful for describing genetic diversity in dynamic landscapes.

Under an infinite alleles model Wright's inbreeding coefficient, the probability that two alleles chosen at random from within a breeding group are identical by descent, was estimated as: $F = 1 - H_O$ (Miller and Lacy 2005), where H_O equals the average observed frequency of heterozygous individuals within a breeding group.

Simulations

The RCW IB-SEPM was run for 100 years for all landscapes. The simulations were run for baseline and status quo landscape conditions assuming that the territory configuration remained constant over time. The other landscapes were created by simulating the habitat trading scenario in which habitat was added or removed from the status quo landscape at different times, as discussed above.

The model is stochastic, so we repeated each simulation 100 times and examined the distribution of outcomes. Population extinction occurred when only one breeding group remained and no subsequent breeding groups are formed. H_S, D_{ST}, and N (abundance) were tracked over time. Territory summaries were also calculated at year 75 to contrast landscapes based on the probability that an individual territory would be vacant and Wright's inbreeding coefficient.

LEA accounting

A "LEA credit" represents the marginal contribution a change in landscape structure (i.e., taking or restoring of habitat) makes toward moving the ecological service closer to service levels observed in a baseline landscape. For the mitigation landscape, the number of LEA credits available in the bank at the time of the trade ($t = 25$) was estimated as Landscape Service Years (Bruggeman et al. 2005), which is a time-integrated estimate of the proportional change in ecological services relative to the sustainability goal due to marginal change in landscape structure. The expected number of abundance credits is estimated as Landscape Service Years—Abundance (LSY_C^N):

$$E\left[LSY_C^N\right] = \sum_{t=W}^{100} \left(\frac{m_t^N - j_t^N}{b_t^N} \right) \qquad (1)$$

where W is the time the trade occurs, b_t^N is the expected total abundance in breeding groups at year t provided by the baseline landscape, m_t^N is the expected total abundance in breeding groups at year t provided by the mitigation landscape, and j_t^N is the expected total abundance in breeding groups at year t provided by the status quo landscape.

The number of credits purchased to offset the local and regional loss of abundance due to a withdrawal, or the debit from the bank, can be calculated as Landscape Service Years—Abundance (LSY_D^N):

$$E\left[LSY_D^N\right] = \sum_{t=W}^{100} \left(\frac{m_t^N - w_t^N}{b_t^N} \right) \qquad (2)$$

where w_t^N is the expected abundance at year t provided by the withdrawal landscape.

Calculating credits associated with changes in genetic variance is more complex. The management goal is to approximate population services provided by the distribution of habitat in which the organism evolved (Meffe 1996). Greater genetic diversity within a breeding group or greater genetic divergence among breeding groups is not always better for sustainability (Bouzat 2001). The levels of genetic service provided by the baseline landscape will be used to direct trading toward this goal. As estimates of genetic variance within and among breeding groups move closer to baseline levels due to restoring habitat area or connectivity, the more credit is accrued in the bank. The credit representing a marginal change in genetic services associated with the mitigation landscape can be calculated as Landscape Service Years—Genetic Variance (LSY_C^G):

$$E\left[LSY_C^G\right] = \sum_{t=W}^{100} \left(\frac{\left| b_t^G - j_t^G \right|}{b_t^G} \right) - \sum_{t=W}^{100} \left(\frac{\left| b_t^G - m_t^G \right|}{b_t^G} \right) \qquad (3)$$

where G is the genetic variance component estimated (H_S or D_{ST}), b_t^G is the expected level of genetic variance at year t provided by the baseline landscape, j_t^G is the expected level of genetic variance at year t provided by the status quo landscape, and m_t^G is the expected level of genetic variance at year t provided by the mitigation landscape. The first summation reports the extent of habitat fragmentation present in the landscape prior to mitigation. The second summation, to the right of the minus sign, reports the level of fragmentation after a bank is established. LSY_C^G then equals the degree to which bank establishment reverses the effects of fragmentation.

The number of credits purchased to offset the withdrawal or departure of genetic variance away from baseline-levels relative to mitigation-levels can be calculated as Landscape Service Years—Genetic Variance (LSY_D^G):

$$E\left[LSY_D{}^G\right] = \sum_{t=W}^{100} \left(\frac{\left|b_t^G - w_t^G\right|}{b_t^G} \right)$$
$$- \sum_{t=W}^{100} \left(\frac{\left|b_t^G - m_t^G\right|}{b_t^G} \right) \qquad (4)$$

where w_t^G is the expected level of genetic variance at year t reflecting anticipated loss of habitat area or connectivity. LSY_D^G equals the debit that results when the withdrawal moves the balance between recruitment and migration farther away from baseline levels due to the "take" (i.e., the change in fragmentation that results from a withdrawal).

Results

The observed frequency of heterozygotes within breeding groups did not deviate significantly from expectations under Hardy–Weinberg Equilibrium for most landscapes and dispersal assumptions based on a Chi squared test ($P > 0.05$) (Li and Horvitz 1953). Observed frequency of heterozygotes within breeding groups did deviate from Hardy–Weinberg expectations during the last 12 years of the status quo landscape under random-straight dispersal ($P < 0.05$). In these cases average observed heterozygosity exceeds expected heterozygosity due to the presence of inbreeding avoidance behaviors included in the simulation. Hardy–Weinberg Equilibrium is not a necessary condition for estimating H_S and D_{ST} (Nei 1973, 1986). When not in Hardy–Weinberg Equilibrium Nei's estimate of H_S equals the genetic diversity within groups, or the probability of choosing two alleles at random that are independent, but not the expected heterozygosity.

First we contrast results for the two simulations in which landscape structure did not change over time (i.e., baseline and status quo). In the baseline landscape, we found that genetic variance within and among groups was maintained while minimizing inbreeding when a continuous distribution of longleaf pine habitat exists (Figs. 2, 3). This is an emergent property of the models indicating that the RCW mating system of male philopatry and female dispersal led to a balance between rates of recruitment and migration that maintained genetic variance

at two spatial scales. Therefore, the landscape in Fig. 1b served as an adequate baseline for this analysis. However, when RCWs were subjected to a discontinuous distribution of habitat, but with the same overall habitat area (i.e., status quo), rates of inbreeding and probability of territory vacancy increase dramatically under the forest-based dispersal model (Fig. 3). In contrast, under the random-straight model inbreeding does not increase but probability of territory vacancy does increase dramatically.

When habitat restoration was added to the status quo landscape (Fig. 1c, mitigation landscape) a greater increase in probability of persistence resulted under the assumption of random-straight dispersal (Table 1). The population tended to be more persistent in the status quo landscape under the assumption of forest-based dispersal, likely due to greater retention of floaters and helpers (Table 1), so the benefit of restoration is smaller. Withdrawal 1 decreased the probability of persistence by roughly an equal proportion of the conservation value added by the bank under both dispersal models ($\sim$ 20%, i.e., 0.11/0.47 for random-straight and 0.05/0.25 for forest-based [Table 1]). Withdrawal 2 created no change in probability of persistence under random-straight dispersal, but actually increased the probability of persistence slightly under forest-based dispersal.

LEA: accruing credits

Ecological service flows moved closer to service levels observed in the baseline landscape with the addition of the bank at year 20, compared to the status quo landscape, under both dispersal models (Fig. 2). The number of credits accrued by the bank (LSY_C) was similar for N across dispersal assumptions, but credits for genetic services varied based on which dispersal model was used to describe the behavior of RCWs (Table 2). More genetic variance credits accrued under the random-straight dispersal model due to restoration because in this case there was a greater loss of total genetic variance (H_T) observed in the status quo landscape (Fig. 2, recall $H_T = H_S + D_{ST}$). More alleles were lost under random-straight dispersal due to the greater loss of breeding groups (Fig. 3) and floaters due to emigration (Table 3). The difference in number of credits accrued between dispersal assumptions was greatest for $LSY^{D_{ST}}$. This indicates that genetic differences
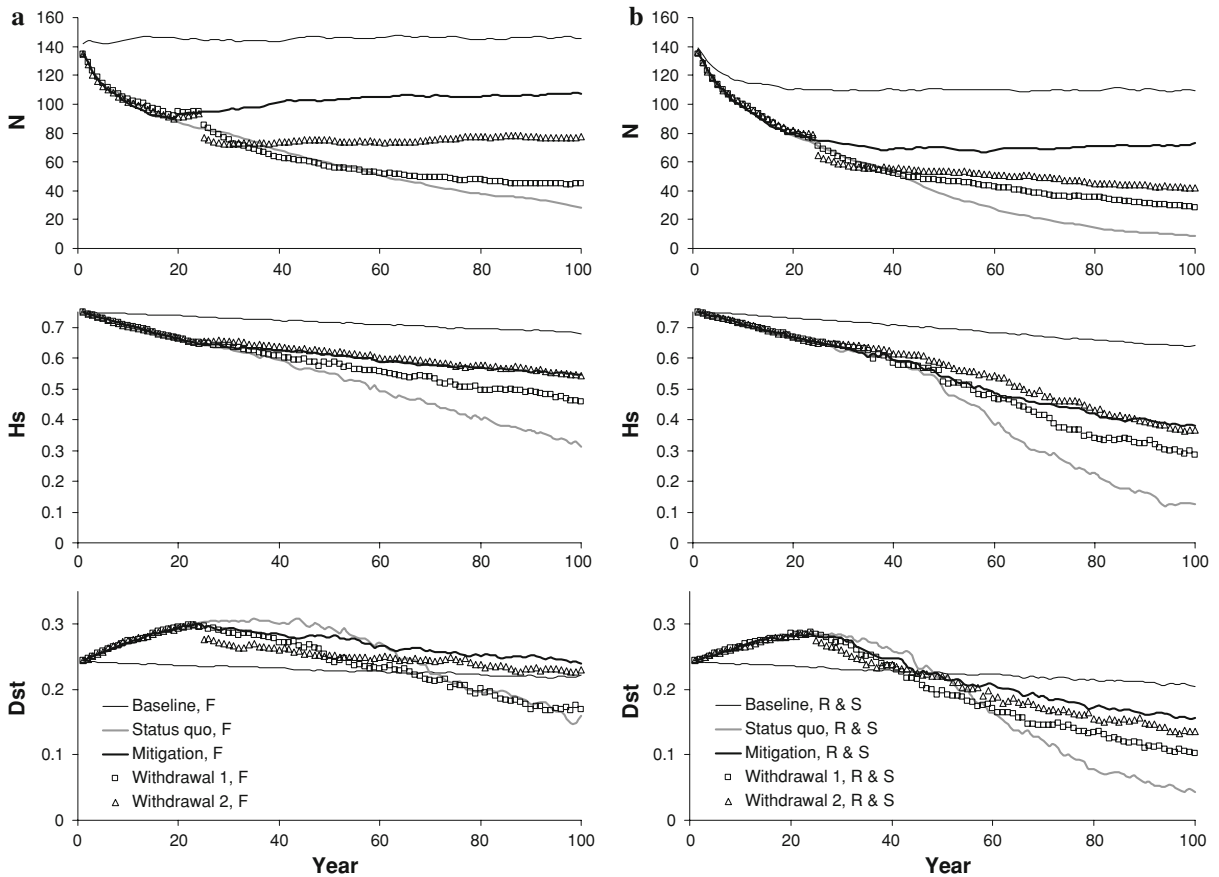
Fig. 2 Ecological service trajectories used to estimate LEA credits (LSYs) assuming two different dispersal strategies: **a** forest-based dispersal and **b** random-straight dispersal. Trajectories represent expected service levels averaged across 100 simulations. N, total abundance in each territory (helpers + breeders); H_S, average expected heterozygosity within breeding groups; D_{ST}, average genetic divergence among breeding groups (Nei 1973)

among breeding groups decreased more with the addition of the bank under random-straight dispersal relative to the status quo landscape, thanks to the longer dispersal distances (Table 3).

LEA: Withdrawal 1

Loss of the 12 most connected territories (w1) under the assumption of random-straight dispersal resulted in a withdrawal of 18.7 of the available abundance credits (Table 2). Therefore, the bank retained a balance of 8.4 credits for abundance. The withdrawal of credits was larger for w1 under the forest-based dispersal model (Table 2), leaving a balance of 1.8 credits.

Under both dispersal models average genetic diversity (H_S) within a territory decreased with the

loss of the 12 most connected territories (w1), but not greater than observed in the status quo landscape (i.e., credits were not overdrawn). Therefore, the 12 most connected territories were positively weighting H_S averaged across the landscape (Petit et al. 1998). In other words, rates of genetic drift and inbreeding were relatively low in the territories lost, so their removal created a debit of genetic services. For the territories that constitute "the bank" rates of inbreeding actually increased in the Withdrawal 1 landscape relative to the mitigation landscape (Fig. 3).

Whether w1 resulted in a net withdrawal or accrual of credits for LSYs$^{D_{ST}}$ depended on which dispersal model was used. The D_{ST} trajectory resulting from w1 was similar across the two alternative dispersal assumptions. However, the status quo and mitigation service levels differed greatly between the dispersal
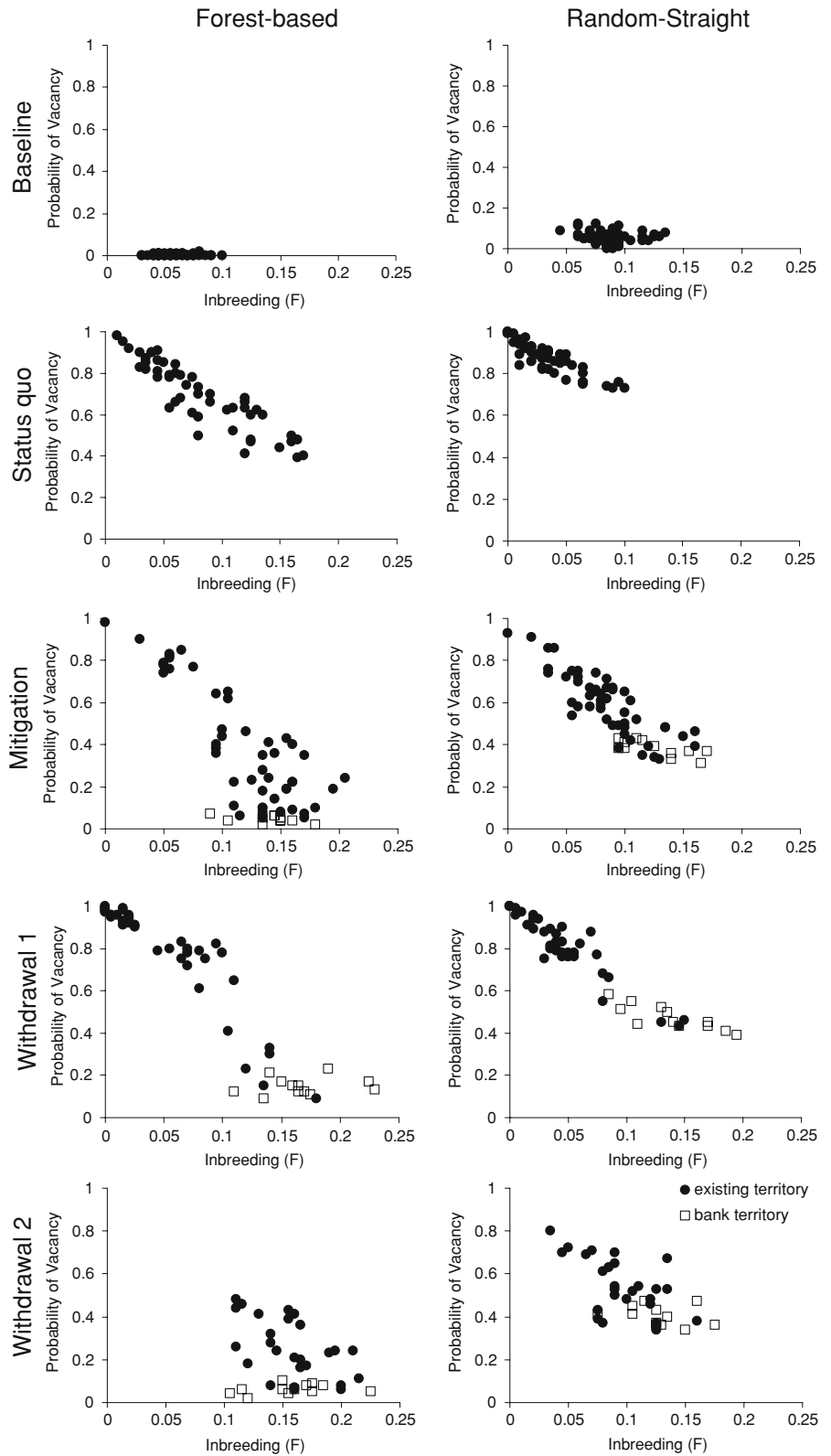
Table 1 Estimated species probability of persistence for the status quo (A), mitigation (C), and the two withdrawal (D, E) landscapes (Fig. 1)

Landscape	Probability of persistence				Value of bank	Decrease due to w1	Decrease due to w2	Value remaining: w1	Value remaining: w2
	Status quo	Mitigation	Withdrawal 1 (w1)	Withdrawal 2 (w2)					
	A	C	D	E	(C − A)	(C − D)	(C − E)	(C − A) − (C − D)	(C − A) − (C − E)
Dispersal strategy									
Forest-based	0.73	0.98	0.93	1.0	0.25	0.05	−0.02	0.20	0.27
Random-straight	0.27	0.74	0.63	0.74	0.47	0.11	0.0	0.36	0.47

Also presented is the estimated value of the conservation bank before and after the two withdrawals and the decrease in bank value due to each withdrawal

assumptions (Fig 2). These differences resulted because probability of territory vacancy was lower under the forest-based model (Fig. 3), because more helpers and floaters were retained on the landscape (Table 3). Therefore a greater loss of total genetic variance resulted under random-straight dispersal. Also shorter dispersal distances were observed under forest-based dispersal (Table 3) leading to more genetic differences among groups. However, addition of the bank in the center of the landscape tended to increase expected maximum female dispersal distance under forest-based dispersal in the mitigation and w1 landscapes but not under random-straight dispersal. The net increase in credits under forest-based dispersal reflected this improvement in landscape function because the w1 trajectory moves closer to baseline levels, on average, than the mitigation levels.

LEA: Withdrawal 2

Loss of the 24 least connected territories (w2) resulted in a larger initial decline in abundance but a smaller withdrawal of credits under both dispersal models (Table 2; Fig. 2), compared to w1. The benefits of restoring 12 well connected bank territories provides sufficient credits to justify the loss of 24 of the least connected territories.

Withdrawal 2 resulted in moving H_S closer to baseline levels under both dispersal models, leading to an accrual of more credits within the bank for this ecological service. Thus, the least connected territories were negatively weighting average genetic diversity within groups compared to territories remaining after the trade (Petit et al. 1998), especially under random-straight dispersal. In other words, the 24 least connected territories tended to have lower genetic diversity within groups, due to combined influence of inbreeding and genetic drift. For the territories remaining after Withdrawal 2, rates of inbreeding within a territory were roughly equivalent to those observed in the mitigation landscape at year 75 (Fig. 3).

As observed in w1, the withdrawal or accrual of credits resulting from w2 depends on the dispersal model for $LSY^{D_{ST}}$ credits. Forest-based dispersal resulted in over a 2-fold increase in credits. This indicates that the 24 isolated territories were positively weighting average genetic divergence among

Table 2 Estimated proportional change in ecological services, reported as Landscape Service Years (LSYs, equations given in text) due to establishment of a conservation bank and two alternative withdrawal scenarios using Landscape Equivalency Analysis

Landscape service years	Value of bank (Eq. 1 or 3)	Decrease due to Withdrawal 1 (Eq. 2 or 4)	Decrease due to Withdrawal 2 (Eq. 2 or 4)	Value remaining: Withdrawal 1	Value remaining: Withdrawal 2
Forest-based dispersal					
LSY^N	26.9	25.1	14.7	26.9 − 25.1 = 1.8	26.9 − 14.7 = 12.2
LSY^{H_S}	11.6	4.5	−1.0	11.6 − 4.5 = 7.1	11.6 + 1.0 = 12.6
$LSY^{D_{ST}}$	2.0	−3.1	−6.4	2.0 + 3.1 = 5.1	2.0 + 6.4 = 8.4
Random-straight dispersal					
LSY^N	27.1	18.7	13.7	27.1 − 18.7 = 8.4	27.1 − 13.7 = 13.4
LSY^{H_S}	13.4	4.0	−2.2	13.4 − 4.0 = 9.4	13.4 + 2.2 = 15.6
$LSY^{D_{ST}}$	18.3	9.6	2.3	18.3 − 9.6 = 8.7	18.3 − 2.3 = 16.0

Three services (i.e., N, abundance; H_S, average genetic diversity within breeding groups; and D_{ST}, average genetic divergence among breeding groups) related to probabilities of population viability were used to quantify Landscape Service Years (LSY^N, LSY^{H_S}, $LSY^{D_{ST}}$, respectively) that differ in sensitivity to changes in habitat area and connectivity

Table 3 Comparison of dispersal and helping behaviors across the landscape configurations used to simulate habitat trades

Landscape	Random-straight		Forest-based	
	Male	Female	Male	Female
Emigration rate[a]				
Baseline	0.66 (0.15)	1.95 (0.29)	0.0003 (0.0017)	0.018 (0.013)
Status quo	0.39 (0.45)	1.18 (1.10)	0.12 (0.12)	0.41 (0.32)
Mitigation	0.53 (0.40)	1.59 (0.85)	0.15 (0.11)	0.50 (0.26)
Withdrawal 1	0.39 (0.45)	1.15 (1.08)	0.09 (0.13)	0.34 (0.37)
Withdrawal 2	0.51 (0.47)	1.37 (0.93)	0.12 (0.16)	0.37 (0.32)
Maximum dispersal distance[b] (m)				
Baseline	8,639 (809)	9,341 (463)	8,095 (876)	9,804 (240)
Status quo	18,868 (3,822)	20,836 (2,657)	14,338 (1,681)	15,253 (1,432)
Mitigation	19,173 (2,716)	20,625 (2,002)	14,745 (1,709)	15,749 (1,299)
Withdrawal 1	18,400 (2,603)	20,372 (2,343)	14,399 (1,901)	15,891 (1,599)
Withdrawal 2	18,612 (2,830)	20,386 (2,269)	13,841 (1,629)	15,183 (1,759)
Average number of helpers per territory				
Baseline	0.26 (0.10)		0.91 (0.025)	
Status quo	0.13 (0.15)		0.22 (0.13)	
Mitigation	0.16 (0.13)		0.27 (0.10)	
Withdrawal 1	0.16 (0.14)		0.26 (0.11)	
Withdrawal 2	0.17 (0.13)		0.28 (0.10)	

Averages were taken across the 100 Monte Carlo simulations applied to each landscape (one sample standard deviation)

[a] Average number of male and female floaters lost as emigrants per year ($n = 100$)

[b] Average maximum dispersal distance traveled by floaters from their natal territory to breeding territory ($n = 100$)

territories in the mitigation landscape under forest-based dispersal. Therefore, their loss pulled D_{ST} closer to levels observed in the baseline landscape, while decreasing the probability of territory vacancy (Fig. 3). Random-straight dispersal resulted in a small withdrawal of credits. Under random-straight dispersal these territories also positively weighted D_{ST} averaged across the landscape. But the greater loss of total

genetic diversity due to probability of territory vacancy (Fig 3) under this dispersal assumption resulted in pulling D_{ST} farther away from both baseline and mitigation levels.

Withdrawal 2 led to a smaller withdrawal of LEA credits from the bank and a smaller change in probability of persistence than Withdrawal 1 under both dispersal models. Withdrawal 2 also moved rates of inbreeding and probability of territory vacancy closer to levels observed in the baseline landscape (Fig. 3).

Discussion

In simulations for both withdrawals, probabilities of persistence did not decrease below levels expected in the status quo landscape. Therefore, trading did not violate jeopardy standards. However, we observed that probability of persistence, when evaluated alone, was a crude indicator of patch conservation value. For example, there was no difference between probability of persistence in the Withdrawal 2 and the mitigation landscape assuming random-straight dispersal. This result would lead a practitioner to believe that the 24 least connected patches made no contribution to population viability (i.e., their conservation value = 0). However, LEA results indicated that the conservation value of these patches depends on which services are evaluated. The 24 least connected patches are often occupied because their loss does create a debit for abundance. Further, these patches contributed to maintaining genetic divergence among breeding groups closer to levels observed in the baseline landscape (Fig. 2b).

Under LEA, credits are accrued as landscape change moved the balance between migration and drift closer to levels observed in the baseline landscape. When a positive balance of credits remained it meant that despite the trade, the bank had still moved rates of recruitment and/or migration closer to baseline than would be expected had no mitigation been implemented (i.e., status quo landscape). When habitat loss actually increased the number of credits in a bank (i.e., a negative LSY_D^G value), the change in landscape structure moved rates of recruitment and/or migration closer to levels observed prior to habitat loss and fragmentation (i.e., baseline), than observed in the mitigation landscape.

For example, under forest-based dispersal a net increase in D_{ST} credits resulted from both withdrawals. Under forest-based dispersal greater habitat density limits the exchange of alleles over space, because individuals move shorter distances due to their attraction to breeding habitat. This leads to greater genetic differences among groups in a fragmented landscape. By restoring pine in the center of the landscape individuals are more likely to spread across the landscape. Therefore, under forest-based dispersal the bank acts as a stepping stone and alleles are shared more evenly among groups, as observed in the baseline landscape. In contrast, under random-straight dispersal both trades led to a net withdrawal of credits because land use classes do not directly affect dispersal behaviors.

Results of this study show that in an unfragmented landscape RCW natural history traits do minimize risks from local extinction and inbreeding ($F \leq 0.125$; Daniels and Walters 2000) while maintaining genetic variance among breeding groups (Figs. 2, 3). In the baseline landscape the apportionment of genetic diversity under both dispersal models closely approximated the level observed in an Island Model (Wright 1931) assuming one migrant per generation ($F_{ST} = 1 - H_S/H_T = 0.24 =$ proportion of total genetic diversity due to population subdivision). These results confirm Wright's intuition that $0.2 < F_{ST} < 0.25$ reduces threats from drift and inbreeding while maintaining opportunities for adaptation (Mills and Allendorf 1996). These results are not too surprising as RCWs evolved in a fairly continuous distribution of longleaf pine savannah and the USFWS recommends maintaining a clumped distribution of habitat (USFWS 2003b).

Policy considerations

Bruggeman et al. (2005) proposed setting a limit on access to the landscape by stating that trades should not produce an allocation of habitat that drives the spatial apportionment of genetic variance farther away from baseline levels (i.e., max $|b^G - j^G| \geq$ max $|b^G - w^G|$ to allow trade). Figure 2 indicates that this rule was not violated; the trades did not skew the spatial allocation of variance farther away from baseline compared to the status quo landscape. We feel this could be an important addition to endangered species policy as it prevents trades that move rates of

recruitment and migration farther away from baseline levels than were previously observed in the status quo landscape. No regulatory criteria for managing changes in functional fragmentation of habitat are included in the ESA (USFWS 1973). Application of the take standard could lead to banks that serve as sinks (Pulliam 1988) (i.e., banks remain occupied but do not contribute to dispersal among groups and thus sustainability of population across the landscape). Probability of persistence might capture this if sink effects are sufficient to change extinction risk at a landscape-scale, but this is not guaranteed.

Opportunities for adaptive management

The required monitoring of the outcomes of mitigation under ESA's Sect. 10 (USFWS 1973) provides an opportunity to learn about interactions between landscape patterns and biological processes in dynamic landscapes. We included uncertainty by using expectations from two alternative hypotheses to evaluate two habitat trades. Some important differences between the models were observed. Compared to the current assumptions regarding dispersal used for landscape-scale management (USFWS 2003b), incorporating a new dispersal hypothesis (i.e., forest-based), increased the number of $LSY^{D_{ST}}$ available in the bank, increased the number of LSY^{N} withdrawn, and decreased the probability of extinction. The largest difference in exchange of LEA credits based on the alternative dispersal models was observed for $LSY^{D_{ST}}$ (Table 2). Therefore, the ecological services used in LEA differ in sensitivity to assumptions regarding biological processes (Bruggeman et al. 2005).

When appropriately implemented, tradable credit systems provide financial mechanisms for reducing uncertainty. USFWS (2003a) proposed incorporating risks associated with a habitat trade into the price of credits to offset costs of the endowment used for management. Our results suggest that updating model assumptions as monitoring data accrue could lead to a decrease in the size of the required endowment. Specifically, if we learn that the true state of nature is more likely to be forest-based dispersal, our simulations suggest that habitat trading would have a smaller impact on extinction risk, and should decrease the size of endowment maintained by the bank.

Integration of financial tools with more scientifically rigorous approaches to conservation banking will require creative policies that balance the sustainability of the species with the sustainability of conservation banking market. Using the most up-to-date knowledge regarding the response of a population, which may or may not be functioning as a metapopulation, to changes in landscape structure when siting a bank would contribute to both population and financial sustainability. Requiring that models be updated with the latest natural history information prior to a trade would increase transaction costs and may decrease the conservation value of a bank. Regulatory assurances could be put in place to prevent a decrease in bank value as knowledge accrues. However, the acquired knowledge of the system should be used when establishing new banking agreements and planning recovery actions.

Conclusion

We have described how access to a landscape can be limited and allocated among resource users by integrating IB-SEPMs, population genetic theory, and natural resource economics. The regional ecological effects of local trades are internalized by a market for LEA credits. Therefore, if loss of one patch reduces the probability of habitat occupancy or increases rates of inbreeding for a neighboring patch, the habitat bank must provide a sufficient increase in rates of habitat occupancy and outbreeding across the landscape to justify the individual trade. Therefore, LEA provides a method for allocating access rights to habitat at a local scale without decreasing regional population viability.

References

Bayon R (2002) A bull market in … woodpeckers? Milliken Inst Rev 4:30–39

Bell SS, Fonseca MS, Motten LB (1997) Linking restoration and landscape ecology. Restor Ecol 5:318–323. doi: 10.1046/j.1526-100X.1997.00545.x

Bouzat JL (2001) The importance of control populations for the identification and management of genetic diversity. Genetica 110:109–115. doi:10.1023/A:1017985522650

Brook BB, O'Grady JJ, Chapman AP et al (2000) Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387. doi:10.1038/35006050

Bruggeman DJ, Jones ML (2008) Should habitat trading be based on mitigation ratios derived from landscape indices: a model-based analysis of compensatory restoration options for the Red-cockaded Woodpecker. Environ Manag 42:591–602. doi:10.1007/s00267-008-9179-2

Bruggeman DJ, Jones ML, Lupi F et al (2005) Landscape equivalency analysis: methodology for calculating spatially-explicit biodiversity credits. Environ Manag 36:518–534. doi:10.1007/s00267-004-0239-y

Conner RN, Rudolph DC (1991) Forest habitat loss, fragmentation, and Red-cockaded Woodpecker populations. Wilson Bull 103:446–457

Daniels SJ, Walters JR (2000) Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. Condor 102:482–491. doi:10.1650/0010-5422(2000)102[0482:IDAIEO]2.0.CO;2

Daniels SJ, Priddy JA, Walters JR (2000) Inbreeding in small populations of Red-cockaded Woodpeckers: insights from a spatially explicit individual-based model. In: Young AG, Clarke GM (eds) Genetics, demography, and viability of fragmented populations. Cambridge University Press, New York, pp 129–148

deGroot RS, Wilson MA, Boumans RMJ (2002) A typology for the classification, description and valuation of ecosystem functions, goods, and services. Ecol Econ 41:393–408

Engstrom RT, Sanders FJ (1997) Red-cockaded foraging ecology in an old-growth longleaf pine forest. Wilson Bull 109:203–217

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fox J, Nino-Murcia A (2005) Status of species conservation banking in the United States. Conserv Biol 19:996–1007

Frost CC (1993) Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc Tall Timbers Fire Ecol Conf 18:17–44

Grimm V, Revilla E, Berger U et al (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecol Appl 12:321–334

Hanski I, Gaggiotti OE (2004) Metapopulation biology: past, present, and future. In: Hanski I, Gaggiotti OE (eds) Ecology, genetics, and evolution of metapopulations. Elsevier Academic Press, San Diego, pp 3–22

Hastings HM, Sugihara G (1993) Fractals: a user's guide for the natural sciences. Oxford University Press, New York

Jones CA, Pease KA (1997) Restoration-based compensation measures in natural resource liability statutes. Contemp Econ Policy 15:111–122

Letcher BH, Priddy JA, Walters JR et al (1998) An individual-based, spatially-explicit simulation model of the population dynamics of the endangered Red-cockaded Woodpecker, Picoides borealis. Biol Conserv 86:1–14

Li CC, Horvitz DG (1953) Some methods of estimating the inbreeding coefficient. Am J Hum Genet 5:107–117

Lindenmayer DB, Fischer J (2007) Tackling the habitat fragmentation pancheston. Trends Ecol Evol 22:111–166

Lindenmayer DB, Lacy RC (1995) Metapopulation viability of leadbeater's possum, Gymnobelideus leadbeateri, in fragmented old-growth forests. Ecol Appl 5:164–182

Lindenmayer DB, Cunningham RB, MacGregor C et al (2008) Temporal changes in vertebrates during landscape transformation: a large-scale "natural experiment". Ecol Monogr 78:567–590

Loomis JB, White DS (1996) Economic benefits of rare and endangered species: summary and meta-analysis. Ecol Econ 18:197–206

MacNally R, Bennett AF, Horrocks G (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. Biol Conserv 95:7–29

Manel S, Schwartz MK, Luikart G et al (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

Meffe GK (1996) Conserving genetic diversity in natural systems. In: Szaro RC, Johnston DW (eds) Biodiversity on managed landscapes: theory and practice. Oxford University Press, New York, pp 41–57

Miller PS, Lacy RC (2005) VORTEX: a stochastic simulation of the extinction process. Version 9.50 user's manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley

Mills LS, Allendorf FW (1996) The one-migrant-per-generation rule in conservation and management. Conserv Biol 10:1509–1518

Moritz C (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. Syst Biol 51:238–254

Nei M (1973) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70:3321–3323

Nei M (1986) Definition and estimation of fixation indices. Evolution 40:643–645

Petit RJ, Mousadik AE, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. Conserv Biol 12:844–855

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Sala OE, Chapin FSIII, Armesto JJ et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Schrott GR, With KA, King AW (2005) On the importance of landscape history for assessing extinction risk. Ecol Appl 15:493–506

Spielman D, Brook BW, Frankham R et al (2004) Most species are not driven to extinction before genetic factors impact them. Proc Natl Acad Sci USA 101:15261–15264

Stanford Environmnental Law Society (2001) The Endangered Species Act. Stanford University Press, Stanford

Tietenberg T (2004) The tradable permits approach to protecting the commons: what have we learned? Working paper written for National Research Council's Institutions for Managing the Commons Project. www.colby.edu/personal/thtieten/TT.NRC4.pdf Last accessed. May 18, 2007

USFWS (United States Fish and Wildlife Service) (1973) Endangered Species Act of 1973 as amended by 108th Congress. Department of the Interior. Washington, D.C.

USFWS (United States Fish and Wildlife Service) (2003a) Guidance for the establishment, use, and operation of conservation banks. United States Department of the Interior, Washington, D.C.

USFWS (United States Fish and Wildlife Service) (2003b) Recovery plan for the Red-cockaded Woodpecker (*Picoides borealis*): second revision. United States Department of the Interior. Atlanta, GA

Van Horne B (1983) Density as a misleading indicator of habitat quality. J Wildl Manag 47:893–901

Walters JR, Doerr PD, Carter JHIII (1988) The cooperative breeding system of the Red-cockaded Woodpecker. Ethology 78:275–305

Walters JR, Daniels SJ, Carter JHIII et al (2002) Defining quality of Red-cockaded Woodpecker foraging habitat based on habitat use and fitness. J Wildl Manag 66:1064–1082

Wang J (2004) Application of the one-migrant-per-generation rule to conservation and management. Conserv Biol 18:332–343

Wright S (1931) Evolution in Mendelian populations. Genetics 16:97–159