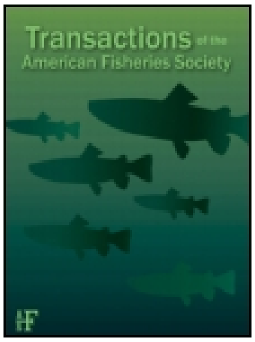

Transactions of the American Fisheries Society

ISSN: 0002-8487 (Print) 1548-8659 (Online) Journal homepage: http://www.tandfonline.com/loi/utaf20

Landscape-Scale Evaluation of Asymmetric Interactions between Brown Trout and Brook Trout Using Two-Species Occupancy Models

Tyler Wagner , Jefferson T. Deweber , Jason Detar & John A. Sweka

Transactions of the American Fisheries Society 142:353–361, 2013

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.734892

ARTICLE

Landscape-Scale Evaluation of Asymmetric Interactions between Brown Trout and Brook Trout Using Two-Species Occupancy Models

Tyler Wagner*
U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, 402 Forest Resources Building, University Park, Pennsylvania 16802, USA

Jefferson T. Deweber
Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, Pennsylvania 16802, USA

Jason Detar
Pennsylvania Fish and Boat Commission, 450 Robinson Lane, Bellefonte, Pennsylvania 16823, USA

John A. Sweka
U.S. Fish and Wildlife Service, Northeast Fishery Center, Post Office Box 75, 308 Washington Avenue, Lamar, Pennsylvania 16848, USA

Abstract
Predicting the distribution of native stream fishes is fundamental to the management and conservation of many species. Modeling species distributions often consists of quantifying relationships between species occurrence and abundance data at known locations with environmental data at those locations. However, it is well documented that native stream fish distributions can be altered as a result of asymmetric interactions between dominant exotic and subordinate native species. For example, the naturalized exotic Brown Trout *Salmo trutta* has been identified as a threat to native Brook Trout *Salvelinus fontinalis* in the eastern United States. To evaluate large-scale patterns of co-occurrence and to quantify the potential effects of Brown Trout presence on Brook Trout occupancy, we used data from 624 stream sites to fit two-species occupancy models. These models assumed that asymmetric interactions occurred between the two species. In addition, we examined natural and anthropogenic landscape characteristics we hypothesized would be important predictors of occurrence of both species. Estimated occupancy for Brook Trout, from a co-occurrence model with no landscape covariates, at sites with Brown Trout present was substantially lower than sites where Brown Trout were absent. We also observed opposing patterns for Brook and Brown Trout occurrence in relation to percentage forest, impervious surface, and agriculture within the network catchment. Our results are consistent with other studies and suggest that alterations to the landscape, and specifically the transition from a forested catchment to one that contains impervious surface or agriculture, reduces the occurrence probability of wild Brook Trout. Our results, however, also suggest that the presence of Brown Trout results in lower occurrence probability of Brook Trout over a range of anthropogenic landscape characteristics, compared with streams where Brown Trout were absent.

*Corresponding author: txw19@psu.edu
Received June 20, 2012; accepted September 25, 2012
Published online January 22, 2013

Attempting to quantify and understand abiotic and biotic factors influencing the distribution of native stream fish species across the landscape is a high priority for fisheries ecologists and managers. One of the primary classes of models that relate information about species occurrence and abundance data at known locations with environmental data at those locations are species distribution models (Elith and Leathwick 2009). This class of models is commonly used to make inferences about the current status of fish species, in addition to making inferences about potential changes in distribution under forecasted climate and land use change scenarios (Elith and Leathwick 2009; Bond et al. 2011; Wenger et al. 2011). Although species distribution models have proven very useful, there remain challenges in their application. One challenge in particular is accounting for biotic interactions, including competition and predation, when predicting the distribution of a species (Elith and Leathwick 2009). It is widely accepted that biotic interactions can play an important role in structuring stream fish communities (Fausch and White 1981; Gilliam and Fraser 2001): interactions that often result in one species having a lower occurrence probability at stream sites where a competitor or predator is present than at sites where the competitor or predator is absent. To date, however, stream fish species distribution models rarely explicitly account for co-occurrence patterns between species.

The use of detection–nondetection (i.e., presence–absence data) data are often used to develop stream fish species distribution models largely because presence–absence data are more readily available over large spatial extents than catch per effort or abundance estimates and because site occupancy is, in general, a useful indicator of population status (Royle et al. 2005). Although some studies have examined co-occurrence patterns among stream fish species (Peres-Neto 2004; de la Hoz and Budy 2005; Hoeinghaus et al. 2007), most studies that use presence–absence data fail to account for the fact that detectability of most species is imperfect. Species distribution models that use presence–absence data should, if possible, account for the fact that a species is not always detected where it occurs (MacKenzie et al. 2002). Until recently, this imperfect detectability further complicated the ability to elucidate patterns in co-occurrence while simultaneously examining the effects of additional covariates that were hypothesized to be important factors for predicting occurrence (e.g., land use and cover characteristics). A new parameterization of a model for estimating co-occurrence was recently developed by Waddle et al. (2010) that addressed these complications, providing a powerful approach for species distribution modeling that accounts for co-occurrence patterns. The model specifically addresses a situation where asymmetric interactions are expected to be important, i.e., where the presence of one species (the “dominant” species) is expected to affect the occupancy of another species (the “subordinate” species), but the subordinate species occurrence is not expected to affect the occurrence of the dominant species. This situation is likely to occur in freshwater stream fish communities, especially in the presence of invasive or naturalized exotic species. For instance, the replacement of native Cutthroat Trout *Oncorhynchus clarkii* by nonnative Brook Trout *Salvelinus fontinalis* in the western United States and the reduction or loss of many native fish species in the southern hemisphere by Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta* are largely due to asymmetric interactions between dominant exotics and subordinate natives (Peterson et al. 2004; Young et al. 2010). These potential asymmetric interactions are not only limited to lotic systems. Sharma et al. (2009) predicted that nearly 9,700 Lake Trout *Salvelinus namaycush* populations in Canada may be threatened by the potential range expansion of invasive Smallmouth Bass *Micropterus dolomieu* by 2100.

In the United States, naturalized Brown Trout have been identified as a threat to native Brook Trout (hereafter referred to as Brook Trout) populations (EBTJV 2008). Although the exact mechanisms are unclear, the replacement of Brook Trout by Brown Trout is likely a result of asymmetric interactions (Waters 1999). Accordingly, research addressing interactions between Brook Trout and naturalized Brown Trout has received much attention (e.g., Fausch and White 1981; DeWald and Wilzbach 1992; Zimmerman and Vondracek 2007). The results of these studies suggest that Brook Trout and Brown Trout fulfill similar niches (Zimmerman and Vondracek 2007) and that Brown Trout often retain a competitive advantage over Brook Trout (Fausch and White 1981; DeWald and Wilzbach 1992). Because of these asymmetric interactions, we assumed that Brown Trout were dominant and Brook Trout subordinate under most conditions (Fausch and White 1981; DeWald and Wilzbach 1992). As such, we predicted that the occurrence probability of Brook Trout would be less at sites where Brown Trout were present when compared with sites where Brown Trout were absent.

In addition to interactions with Brown Trout, changes in habitat conditions have been implicated in the decline of Brook Trout populations and in the replacement of Brook Trout populations by Brown Trout (Waters 1983; Krueger and May 1991). Therefore, we also predicted that natural and anthropogenic landscape characteristics would be important predictors of the occurrence of both species. Modeling both the effect of Brown Trout occurrence and landscape characteristics on Brook Trout occupancy is important because failing to account for the effect of Brown Trout occupancy on Brook Trout occurrence could result in misleading inferences related to the effects of changes in land use and cover alone on Brook Trout occupancy.

It has been demonstrated that even moderate increases in catchment urbanization and agriculture can impair stream fish communities. In particular, impervious surface within the stream catchment can lead to a decrease in occurrence of many species (Wenger et al. 2008). This effect is particularly evident where changes to thermal regimes and hydrology reduce the ability of systems to support coldwater species. For example, Wang et al. (2003) found that low levels of urban development (between 6% and 11%) could impair coldwater trout streams in Minnesota and Wisconsin. Road crossings have also been shown to negatively impact Brook Trout populations (Pépino et al. 2012). In addition, agricultural activities within catchments can impair streams through a variety of mechanisms (Allan et al. 1997); Brook Trout were found less often when agricultural land cover exceeded 9.2% of the watershed area and were very unlikely when it was above 35% (Utz et al. 2010). Therefore, we examined several landscape characteristics for modeling Brook and Brown Trout occurrence that represented impacts due to increased anthropogenic presence within the catchment.

The objective of this study was to model the occurrence of Brook Trout at sites with and without Brown Trout, under the assumption that within the Brook Trout's native range, asymmetric interactions occur between the two species. To the best of our knowledge, no study has evaluated large-scale patterns of co-occurrence to quantify the potential effects of Brown Trout presence on Brook Trout occupancy. Much of the research on Brook and Brown Trout interactions has been conducted in laboratory studies, in a single stream, or in a subset of streams.

METHODS

Fish surveys.—Occurrence data collected from 2007 to 2011 for both wild Brook and Brown Trout were obtained from the Pennsylvania Fish and Boat Commission (PFBC). Data for Rainbow Trout were not included in the analysis because wild Rainbow Trout populations are rare in Pennsylvania (Kocovsky and Carline 2005; PFBC, unpublished data). In an effort to ensure that the stream sites we included in the analysis could support trout and, specifically, could support Brook Trout, we screened sites using the following criteria:

1. We selected stream sites where Brook or Brown Trout were sampled by the PFBC over the 5-year time period. This criterion was used to ensure that we included only "trout streams" (e.g., we excluded streams that potentially exceeded thermal tolerance of Brook or Brown Trout or that were heavily impacted by acid mine drainage, etc.).
2. Because Brook Trout are typically found in smaller headwater stream systems in Pennsylvania, we restricted our analysis to streams located in network catchments less than 1,000 km^2 (i.e., we wanted to exclude larger watersheds where Brook Trout would not be found regardless of the presence of Brown Trout). This value was chosen based on the 99% quantile for network catchment areas where Brook Trout were present (J. T. Deweber, unpublished data).

The resulting sample of stream reaches (reaches delineated by the National Hydrography Dataset Plus [NHDPlus]; USEPA and USGS 2005) was located throughout the state of Pennsylvania (Figure 1), and no two sample sites were located within the same stream reach. All fish sampling used standard electrofishing procedures established by the PFBC, including multiple pass removal and mark–recapture estimates of Brook and Brown Trout abundance as well as single pass electrofishing for the determination of the presence of wild trout. Electrofishing for abundance estimation was typically conducted over a standard 300-m reach, whereas electrofishing to determine presence or absence of wild trout was most often conducted over a 100-m reach.

Because it is uncommon for a stream site to be electrofished multiple times within a year, we used annual surveys at each site, over the 5-year time period, as replicate surveys for occupancy models. We made the assumption that this duration of time satisfied the assumption of site-specific closure in occupancy state, given the life histories of these two species. Both Brook and Brown Trout rarely live beyond age 4 in small Pennsylvania

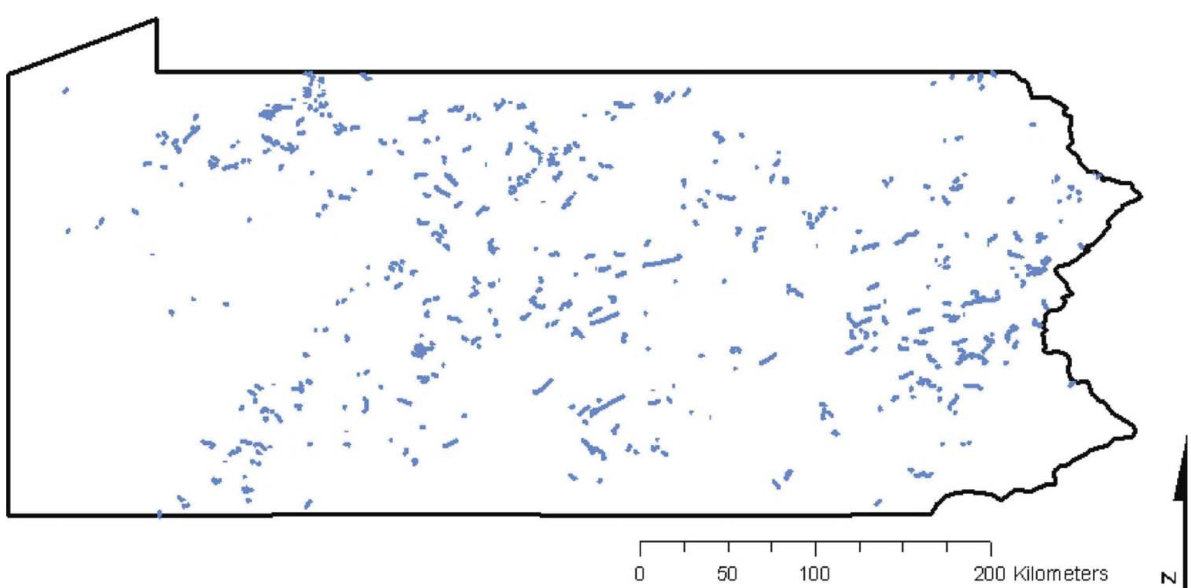

FIGURE 1. Map of Pennsylvania showing the locations of stream reach line segments of sample sites where Brook and Brown Trout were sampled.

streams (McFadden and Cooper 1962; Cooper 1967) and are largely sedentary, although some individuals may move long distances especially during spawning season (Meyers et al. 1992; Roghair and Dolloff 2005; Mollenhauer 2011). To evaluate the sensitivity of our results to this assumption of closure in occupancy state we also performed the analysis using a 3-year time period (2009–2011). Inferences based on the 3-year analysis did not differ from the 5-year analysis; therefore, we present the analysis using the 5-year time period. If the closure assumption was violated, we recognize that this would increase uncertainty in detectability estimates (Wenger et al. 2008).

A total of 624 stream sites were included in the analysis (Figure 1). Of the 624 sites, Brook and Brown Trout were detected at 394 and 416 sites, respectively. Brook Trout were detected during surveys only once at 337 sites, twice at 44 sites, three times at 9 sites, and four times at 4 sites. Brown Trout were detected during surveys only once at 360 sites, twice at 45 sites, three times at 8 sites, and four times at 3 sites. Brook and Brown Trout were found in sympatry at 188 sites.

Landscape covariates.—We used the 1:100,000 NHDPlus stream reaches as the base spatial unit for data management and analysis. Landscape covariates were summarized to the scale of the upstream network catchment for each stream reach. The network catchment was defined as the catchment of the entire river network upstream of each NHDPlus reach. We summarized covariates at only the network catchment scale rather than at the local (i.e., the land area draining directly to a reach) and network catchment scales because local and network landscape summaries were highly correlated for our relatively small stream systems. In addition, we were particularly interested in cumulative upstream impacts on trout occupancy. We included natural and anthropogenic landscape covariates we hypothesized to influence occupancy of Brook and Brown Trout (Table 1). We predicted Brook Trout occupancy would be positively correlated to both forest cover and elevation. For Brown Trout, we predicted a weak positive or negative relationship with both forest cover and elevation, because Brown Trout occur over a wider elevation range and percentage forest cover gradient in Pennsylvania. We predicted, for streams in Pennsylvania, that all anthropogenic landscape characteristics would be negatively related to Brook Trout occurrence, while the effect on Brown Trout would be negative, but of lesser magnitude. As expected, many of these landscape metrics were correlated, an issue that was addressed during model specification.

Model specification.—We fitted two-species occupancy models to examine occupancy of Brook and Brown Trout, under the assumption that occurrence of Brown Trout affected the occurrence and detection probability of Brook Trout (i.e., the interactions between Brook and Brown Trout are asymmetric). The model is described in detail by Waddle et al. (2010). Briefly, the model estimated occupancy (ψ) and detection probability (p) of Brook Trout and Brown Trout simultaneously. While both occupancy and detection probability of Brook Trout were dependent on the presence or absence of Brown Trout, the occupancy and detection probabilities of Brown Trout were not dependent on the presence or absence of Brook Trout. Because we hypothesized that the occurrence of Brook Trout would not only be a function of whether or not Brown Trout were present, we also modeled Brook Trout occupancy as a function of landscape characteristics (Table 1). In addition, we modeled occupancy of Brown Trout as a function of the same landscape characteristics. Estimating the effects of covariates was achieved by expressing occurrence probabilities as linear functions of covariates using a logit link function. We did not model detection probability as a function of covariates because we did not predict that detection would vary according to our landscape covariates. All landscape covariates were transformed prior to analysis. Proportion data were logit-transformed (e.g., percentage forest cover), continuous variables were standardized (scaled to have zero mean and unit variance; e.g., road density), and heavily skewed covariates were $\log_e$ transformed and grand-mean centered (e.g., network percentage impervious surface).

Because many landscape covariates were correlated, we were restricted to fitting models with either one or two covariates. Thus, our model fitting processes included first fitting models with a single landscape covariate for Brook and Brown Trout occupancy. The same covariate was included for each species. Second, we fitted two covariate models, using covariates that had a correlation coefficient (r) <0.60 (Esselman et al. 2011).

TABLE 1. Natural and anthropogenic landscape characteristics, including data source, used to predict occupancy of Brook and Brown Trout in Pennsylvania streams. All metrics were summarized at the network catchment scale.

Landscape characteristic	Mean	SD	Minimum	Maximum	Source
Catchment area (km^2)	61.7	128.6	1.2	958.2	USEPA and USGS 2005
Mean elevation (m)	462.8	150.7	113.1	818.2	USGS 2006
Population density (number/km^2)	30.4	57.0	0.26	481.5	NOAA 2010
Impervious surface (%)	1.2	2.5	0.0	30.6	USGS 2008
Road density (m/km^2)	1,800.0	1,074.0	0.0	7,444.0	USCB 2000
Agriculture (%)	14.7	18.3	0.0	79.0	USGS 2008
Forest (%)	73.7	21.9	3.0	99.0	USGS 2008

Bayesian estimation was used to make inferences about all parameters. Noninformative priors were used and we ran three parallel chains with different initial values to generate 50,000 samples from the posterior distributions for each analysis, after discarding the first 10,000 samples. We retained every 2nd sample. We examined the Gelman–Rubin convergence statistic, chain histories, and posterior density plots to assess convergence. All analyses were performed using the programming environment R and WinBUGS 1.4 (R Development Core Team 2011; Spiegelhalter et al. 2003; R2WinBUGS package; Sturtz et al. 2005).

We used the deviance information criterion (DIC; Spiegelhalter et al. 2002) as a measure of fit to evaluate our set of competing hypotheses. To evaluate the top-ranked models predictive abilities, we calculated a posterior distribution of receiver operating characteristics area under the curve (AUC) following methods outlined in Zipkin et al. (2012). The AUC value ranges from 0 to 1 and measures a model's ability to correctly determine which stream sites are occupied. We calculated AUC to evaluate the top-ranked model's ability to correctly predict locations that were occupied by Brook Trout. A value of 0.5 indicates that the model performs no better than a random guess, while a value of 1.0 implies perfect prediction. Estimated parameters were summarized by computing the posterior means and 80% and 95% credible intervals (CIs).

RESULTS

Estimated occupancy ($\widehat{\psi}$) for Brook Trout, from a co-occurrence model with no landscape covariates (an unconditional model), at sites with Brown Trout present was substantially lower ($\widehat{\psi} = 0.15$; 95% CI = 0.01, 0.41) and had greater uncertainty than sites where Brown Trout were absent ($\widehat{\psi} = 0.98$; 95% CI = 0.93, 1.0). In addition, detection probability ($\hat{p}$) was lower for Brook Trout in sites with Brown Trout present ($\hat{p} = 0.87$; 95% CI = 0.79, 0.93) than sites without Brown Trout ($\hat{p} = 0.99$; 95% CI = 0.98, 1.0), but overall detection was high under both conditions. Estimated occupancy and detection probability for Brown Trout was 0.68 (95% CI = 0.64, 0.72) and 0.95 (95% CI = 0.92, 0.98), respectively (Figure 2). According to this model, of the 624 sites sampled for this study, 422 (95% CI = 406, 445) were estimated to be occupied by Brook Trout and 427 (95% CI = 420, 438) by Brown Trout.

After including landscape-level covariates, the top-ranked model based on DIC was a model that included percentage catchment forest cover for both species (Table 2). This model predicted an increase in Brook Trout occurrence with increasing percentage forest cover, with very low occurrence probabilities (<0.2) of Brook Trout at less than approximately 30% forest and high occurrence probabilities (>0.80) at sites with greater than 60% forest cover in the network catchment. Interestingly, at intermediate ranges of forest cover in the network catchment, from about 30–60% forest, Brook Trout occupancy was lower at sites with Brown Trout present. For example, at 45% catchment forest cover estimated occurrence probability for Brook Trout with Brown Trout present was 0.43 (95% CI = 0.40, 0.46; 80% CI = 0.41, 0.45); while estimated occupancy without Brown Trout was 0.63 (95% CI = 0.54, 0.67; 80% CI = 0.59, 0.66; Figure 2A). Based on this model, of the 624 sites sampled for this study, 481 (95% CI = 461, 501) were estimated to be occupied by Brook Trout and 426 (95% CI = 419, 435) by

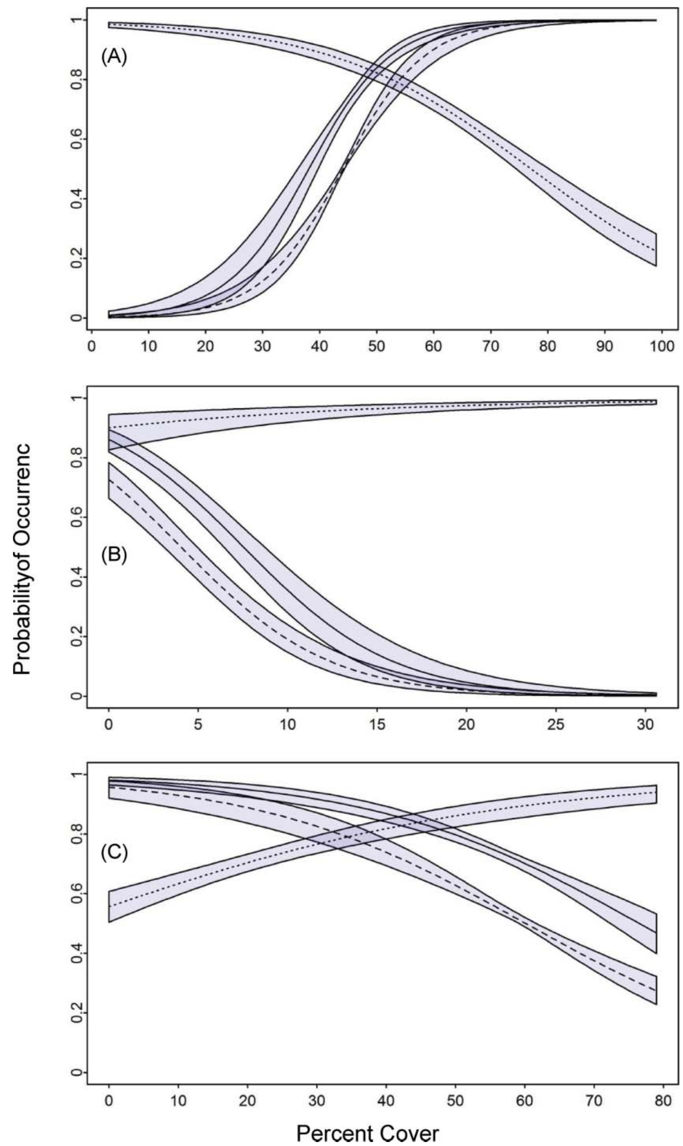

FIGURE 2. Estimated relationship between **(A)** network catchment percentage forest, **(B)** impervious surface, and **(C)** agriculture on Brook Trout occurrence in Pennsylvania streams with (large dashed black line) and without (solid black line) Brown Trout present and Brown Trout occurrence (small dashed line). The thick solid and dashed lines are posterior means and shaded regions are 80% credible intervals. Relationships between occurrence and impervious surface are depicted for network catchments with the average percentage agriculture (14.7%) observed among study catchments, and the relationships between percentage agriculture and occurrence are depicted for network catchments with average percentage impervious surface (1.2%). Note the differences in *x*-axis scales.

TABLE 2. Comparison of models describing occupancy and detection of Brook Trout (with and without the presence of Brown Trout) and Brown Trout in Pennsylvania streams. Models included covariates for Brook and Brown Trout occupancy; detection probability was left unconditional (see Methods). The "+" or "–" sign following the covariate in parentheses indicates the direction of effect. Models are sorted from lowest to highest deviance information criterion (DIC). The unconditional model does not include landscape covariates on occupancy. The posterior mean area under the receiver operating characteristics curve (AUC) is provided for the two top-ranked models, with 95% credible intervals in parentheses.

Brook Trout occupancy covariates	Brown Trout occupancy covariates	Number of parameters	DIC; AUC
percentage forest (+)	percentage forest (–)	8	1,318.4; 0.93 (0.91, 0.95)
percentage impervious (–), percentage agriculture (–)	percentage impervious (+), percentage agriculture (+)	10	1,325.4; 0.94 (0.92, 0.95)
percentage agriculture (–), population density (–)	percentage agriculture (+), population density (+)	10	1,398.9
percentage impervious (–)	percentage impervious (+)	8	1,450.5
mean elevation (+), population density (–)	mean elevation (–), population density (+)	10	1,508.6
percentage agriculture (–), road density (–)	percentage agriculture (+), road density (+)	10	1,527.5
percentage agriculture (–)	percentage agriculture (+)	8	1,546.1
road density (–)	road density (+)	8	1,558.3
mean elevation (+)	mean elevation (–)	8	1,653.7
unconditional	unconditional	6	1,741.8
population density (–)	population density (+)	8	1,808.3
catchment area (–)	catchment area (+)	8	2,038.0

Brown Trout. Brown Trout occupancy was negatively associated with percentage forest cover, with probabilities of occurrence near 1.0 at very low forest cover to <0.3 in heavily forested catchments (Figure 2A).

The second-ranked model included percentage impervious surface and percentage agriculture in the network catchment as predictors of Brook and Brown Trout occupancy. Both covariates were negatively associated with Brook Trout occupancy and positively related to Brown Trout occupancy. The probability of Brook Trout occurrence at sites with Brown Trout present was lower than sites without Brown Trout present at levels of impervious surface up to about 13%. For example, with 0% impervious surface in the catchment (and with average percentage agriculture [14.7%] observed among study catchments), the estimated probability of Brook Trout occupancy with Brown Trout present was 0.73 (95% CI = 0.62, 0.81; 80% CI = 0.66, 0.78; Figure 2B), compared with 0.86 (95% CI = 0.79, 0.91; 80% CI = 0.82, 0.89) when Brown Trout were absent. There was no additional effect of Brown Trout presence on Brook Trout occurrence at high (>13%) levels of impervious surface in the network catchment. The effect of percentage agriculture was not as large when compared with percentage impervious surface, with Brook Trout occupancy still >0.2 at over 70% agriculture in the network catchment (Figure 2C). The effect of Brown Trout presence was evident at levels of agriculture >25% in the network catchment, with sites containing Brown Trout having lower Brook Trout occurrence probabilities (Figure 2C). The effect of impervious surface and agriculture was weak and positive for Brown Trout occurrence. Brown Trout occurrence probabilities were relatively high over the range of impervious surface and agriculture examined, increasing from about 0.90 to 0.99 with increasing percentage impervious surface and from about 0.56 to 0.94 with increasing percentage agriculture (Figure 2C). The directions of effects for the other covariates examined, in lower-ranked models, were also in opposing directions for Brook Trout versus Brown Trout (Table 2). Based on AUC values, both top-ranked models performed well at correctly predicting locations that were occupied by Brook Trout (Table 2).

DISCUSSION

Examining patterns of co-occurrence of Brook and Brown Trout at a landscape scale provided additional evidence that interactions between Brook and Brown Trout may ultimately contribute to Brown Trout replacing Brook Trout in many stream systems. Although this is an observational study, it does supports previous experimental and observational research on the potential influence of Brown Trout presence on Brook Trout occupancy. It is unclear whether Brown Trout have a higher occurrence probability in systems more influenced by agriculture and urbanization because these systems are more suitable for this species (this seems unlikely given their ecological traits) or because propagule pressure is higher in disturbed habitat. Brown Trout have been naturalized in Pennsylvania since the late 1800s and are stocked in some Pennsylvania streams to create seasonal fisheries, primarily in waterways that become too warm to support trout populations year-round. It is evident from our analysis that Brown Trout have an additive impact on Brook Trout in streams with marginally suitable habitat for Brook Trout. Our results do not suggest, however, that Brook Trout are negatively impacted in more natural habitats. This may be due to the ability of Brook Trout to outcompete Brown Trout in more natural habitats, or because propagule pressure has been lower in these systems. Regardless of the exact mechanism, whether it is related to competition, predation, or other interactions, Brown Trout presence appears to be related to a reduced probability of occurrence for Brook Trout in the Pennsylvania streams we examined. In addition, Brown Trout presence was associated with lower detection probability of Brook Trout, which could be due to decreasing Brook Trout densities as Brown Trout became established (e.g., see Waters 1983). However, there was large uncertainty associated with this detection probability estimate.

The top-ranked model demonstrated that Brook Trout occupancy was greatest when percentage forest within the network catchment was greater than 60%. This relationship was expected and supports results by Hudy et al. (2008) who found that 94% of "intact" (i.e., of the historical habitat, over 50% supported self-sustaining populations) subwatersheds (12-digit Hydrologic Unit Code) in the eastern United States had >68% forested lands. Hudy et al. (2008) recommend that natural resource managers should consider values of percentage forest cover below 65–70% as "indicating reduced status of a subwatershed." For Pennsylvania streams, our results support this recommendation: below 65–70% forest cover in the network catchment, the probability of Brook Trout occurrence dropped rapidly. Hudy et al. (2008) did not find the presence of exotic fish species (including Brown Trout) within a subwatershed as an important predictor of Brook Trout status. This was attributed to various factors, including the scale of analysis (i.e., species-level interactions may be difficult to detect at the subwatershed scale). Our model, however, predicted Brook Trout occurrence at the individual stream-reach level and supports the contention that Brown Trout presence or absence should be considered as managers attempt to classify the status of Brook Trout catchments.

The observed opposing patterns for Brook and Brown Trout occurrence with percentage forest in the network catchment also support the work by Kocovsky and Carline (2005). Kocovsky and Carline (2005) found that allopatric Brown Trout populations occurred at lower elevations, while Brook Trout composed a majority of the communities at higher elevations. In our analysis, percentage forest was correlated with elevation ($r = 0.68$) and elevation had similar directional effects as percentage forest cover (i.e., Brook Trout occurrence increased with increasing elevation, while Brown Trout occurrence decreased). Kocovsky and Carline (2005) also suggested that base flow pH may affect the distribution of Brook and Brown Trout in Pennsylvania streams and hypothesized that pH may mediate interspecific competitive interactions between these two species. Although we did not have pH data for our study streams, it is possible that pH and other abiotic factors (e.g., stream temperature) mediate interactions between these two species. That said, the modeling approach we used provides useful information on co-occurrence patterns of these two species independent of the exact mechanisms involved.

The second-ranked model demonstrated that Brook Trout occurrence declined with increasing percentage impervious surface and agriculture in the network catchment, while Brown Trout occurrence increased slightly with increases in both of these landscape characteristics. For both covariates, the probability of Brook Trout occurrence was lower at sites where Brown Trout were also present. This Brown Trout effect was most apparent at low to midlevels of percentage impervious surface (up to ∼10% impervious surface) and at a percentage agriculture of greater than ∼30%. Although percentage impervious surface was associated with a decrease in Brook Trout occurrence, we did not observe extremely low probabilities of occurrence at low levels (e.g., 5%) of impervious surface. This contrasts with Stranko et al. (2008) and Wenger et al. (2008), who found very low probabilities of occurrence for stream fishes at impervious surface levels greater than ∼4%. For Brook Trout, Stranko et al. (2008) found they were almost never found in watersheds where percentage impervious surface exceeded 4% in Maryland streams. The difference in the relationship between Brook Trout occurrence and impervious surface between our study and Stranko et al. (2008) may be partly attributed to the landscape context of these two studies. Figure 2B shows the estimated relationships between Brook Trout occupancy and percentage impervious surface at relatively low percentage agriculture levels (∼15%) within the network catchment. If we predict the effect of percentage impervious surface on Brook Trout occupancy at high (e.g., 80%) levels of agriculture within the catchment, then Brook Trout occupancy drops more rapidly with increasing impervious surface. For example, the probability of Brook Trout occupancy at 5% impervious surface and 80% agriculture is approximately 0.15 with Brown Trout present and 0.30 with Brown Trout absent, compared with >0.40 as illustrated in Figure 2B. Thus, the spatial arrangement and composition of different land use and cover in the catchment may interact, in addition to the presence of potential competitors or predators, in determining whether or not Brook Trout will be present. Our results were more consistent with Wang et al. (2001), who found that impervious surface levels between 8% and 12% represent a threshold where urbanization could result in large changes to stream conditions. For our study streams, we observed a fairly steep decline in occurrence probability for Brook Trout at around 5–10% impervious surface for network catchments with average percentage agricultural land use.

In contrast to the relationship between percentage forest and impervious surface, the effect of Brown Trout presence on Brook Trout occurrence was apparent up to the highest levels of percentage agriculture found in our study catchments. At levels of agriculture less than ∼30%, Brook Trout occurrence probability was high regardless of Brown Trout presence. However, at agriculture levels of 30–80%, the probability of Brook Trout occupancy was lower when Brown Trout were also present. We did not observe steep declines in Brook Trout occupancy with increasing percentage agriculture within the network catchment, in fact, when Brown Trout were absent the probability of Brook Trout occurrence at levels of agriculture >70% was still >0.4. Hudy et al. (2008) found that 74% of subwatersheds with extirpated populations had a value of percentage agriculture in the subwatershed of >12%. Again, differences between our study and Hudy et al. (2008) are likely partly due to the spatial scale of analysis. In addition, the objectives between our study and Hudy et al. (2008) were very different. We were interested in quantifying the effect of Brown Trout presence, in addition to landscape covariates, on Brook Trout occupancy in Pennsylvania. Thus, we prescreened our study catchments to ensure that they would support Brook Trout. This contrasts with Hudy et al. (2008), who were interested in summarizing the status of Brook Trout at the subwatershed scale for the entire native range of Brook Trout in the eastern United States. This does, however, highlight the fact that the scale of investigation should match the objectives of the research and management goals.

The model predictions for the probability of occurrence of Brown Trout increased with increasing percentage impervious surface (Figure 2B) and percentage agriculture (Figure 2C). These predictions are specific to stream reaches within the range of cumulative drainage areas included in this analysis. We expect that if reaches with greater percentage impervious surface were examined, the probability of Brown Trout occurrence would eventually decline.

Our modeling exercise was based on the assumption that Brown Trout were dominant over Brook Trout. This assumption was restricted to streams where Brook Trout were native and Brown Trout were introduced (i.e., the eastern United States). Under these conditions, it is generally accepted that Brown Trout dominate Brook Trout and can eventually replace Brook Trout populations (Korsu et al. 2007). In streams located in other regions, such as in northern Europe, the opposite situation can occur, where Brook Trout (the introduced species) replace Brown Trout (the native species; Korsu et al. 2007). Thus, extrapolating results from this study to other systems should be done with caution. Lastly, although no two sample sites were located within the same stream reach, we acknowledge that there may be some spatial autocorrelation, even after using landscape-level covariates, which could result in bias in parameter estimates and our uncertainty estimates.

Our results support much of the existing research suggesting that alterations to the landscape, and specifically the transition from a forested catchment to one that contains urban development (i.e., impervious surface) or agriculture or both, reduces the occurrence probability of Brook Trout. The modeling approach we employed, however, explicitly accounts for imperfect detection and the co-occurrence patterns of Brook and Brown Trout. Results suggest that Brook Trout occupancy can be significantly lower when Brown Trout are present than when Brown Trout are absent, which supports many laboratory studies on the interactions between these two species (e.g., Dewald and Wilzbach 1992) and observational studies on co-occurrence patterns (e.g., Waters 1983). This is particularly relevant given the amount of effort devoted to assessing the current status of Brook Trout and predicting the potential consequences of land use and climate change on the vulnerability and persistence of these populations. Accounting for co-occurrence patterns is not only relevant for Brook Trout but is likely important for many species of management concern, as ranges of many co-occurring species expand and contract in response to anthropogenic activities.

ACKNOWLEDGMENTS

We would like to thank Pennsylvania Fish and Boat Commission staff for completing the many field surveys required for this analysis. We also thank Seth Wenger and an anonymous reviewer for helpful suggestions on an earlier version of this manuscript. We thank Elise Zipkin for assistance with calculating AUC for occupancy models. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Use of trade names does not imply endorsement by the U.S. government.

REFERENCES

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37:149–161.

Bond, N., J. Thomson, P. Reich, and J. Stein. 2011. Using species distribution models to infer potential climate change–induced range shifts of freshwater fish in south-eastern Australia. Marine and Freshwater Research 62:1043–1061.

Cooper, E. L. 1967. Growth and longevity of Brook Trout (*Salvelinus fontinalis*) in populations subjected to light exploitation. Transactions of the American Fisheries Society 96:383–386.

de la Hoz Franco, E. A., and P. Budy. 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environmental Biology of Fishes 72:379–391.

DeWald, L., and M. A. Wilzbach. 1992. Interactions between native Brook Trout and hatchery Brown Trout: effects on habitat use, feeding, and growth. Transactions of the American Fisheries Society 121:287–296.

EBTJV (Eastern Brook Trout Joint Venture). 2008. Conserving the eastern Brook Trout: action strategies. EBTJV, Conservation Strategy/Habitat Work Group, Albany, New York. Available: www.easternbrooktrout.org/docs/EBTJV_Conservation_Strategy_July_08.pdf. (June 2012).

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Esselman, P. C., D. M. Infante, L. Wang, D. Wu, A. R. Cooper, and W. W. Taylor. 2011. An index of cumulative disturbance to river fish habitats of the conterminous United States from landscape anthropogenic activities. Ecological Restoration 29:133–151.

Fausch, K. D., and R. J. White. 1981. Competition between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

Gilliam, J. F., and D. F. Fraser. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology 82:258–273.

Hoeinghaus, D. J., K. O. Winemiller, and J. S. Birnbaum. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. Journal of Biogeography 34:324–338.

Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of Brook Trout in the eastern United States. North American Journal of Fisheries Management 28:1069–1085.

Kocovsky, P. M., and R. F. Carline. 2005. Stream pH as an abiotic gradient influencing distributions of trout in Pennsylvania streams. Transactions of the American Fisheries Society 134:1299–1312.

Korsu, K., A. Huusko, and T. Muotka. 2007. Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. Proceedings of the National Academy of Sciences of the USA 104:9725–9729.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48(Supplement 1):66–77.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

McFadden, J. T., and E. L. Cooper. 1962. An ecological comparison of six populations of Brown Trout (*Salmo trutta*). Transactions of the American Fisheries Society 91:53–62.

Meyers, L. S., T. F. Thuemler, and G. W. Kornely. 1992. Seasonal movements of Brown Trout in northeast Wisconsin. North American Journal of Fisheries Management 12:433–441.

Mollenhauer, R. 2011. Seasonal movement and habitat use of wild Brook Trout (*Salvelinus fontinalis*). Master's thesis. Pennsylvania State University, University Park.

NOAA (National Oceanic and Atmospheric Administration). 2010. Development sprawl impacts on the terrestrial carbon dynamics of the United States: data download. NOAA, Silver Spring, Maryland. Available: www.ngdc.noaa.gov/dmsp/download_sprawl.html. (June 2012).

Pépino, M., M. A. Rodríguez, and P. Magnan. 2012. Impacts of highway crossings on density of brook charr in streams. Journal of Applied Ecology 49:395–403.

Peres-Neto, P. R. 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. Oecologia 140:352–360.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of Brook Trout on native Cutthroat Trout. Ecological Applications 14:754–772.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org/. (June 2012).

Roghair, C. N., and C. A. Dolloff. 2005. Brook Trout movement during and after recolonization of a naturally defaunated stream reach. North American Journal of Fisheries Management 25:777–784.

Royle, J. A., J. D. Nichols, and M. Kéry. 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110:353–359.

Sharma, S., D. A. Jackson, and C. K. Minns. 2009. Quantifying the potential effects of climate change and the invasion of Smallmouth Bass on native Lake Trout populations across Canadian lakes. Ecography 32:517–525.

Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society B 64:583–639.

Spiegelhalter, D. J., A. Thomas, N. Best, and D. Lunn. 2003. WinBUGS user manual, version 1.4. University of Cambridge Institute of Public Health, MRC Biostatistics Unit, Cambridge, UK.

Stranko, S. A., R. H. Hilderbrand, R. P. Morgan II, M. W. Staley, A. J. Becker, A. Roseberry-Lincoln, E. S. Perry, and P. T. Jacobson. 2008. Brook Trout declines with land cover and temperature changes in Maryland. North American Journal of Fisheries Management 28:1223–1232.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software [online serial] 12:article 3.

USCB (U.S. Census Bureau). 2000. Census 2000 TIGER/line data. USCB, Washington, D.C. Available: www.esri.com/data/download/census2000-tigerline/index.html. (June 2012).

USEPA (U.S. Environmental Protection Agency) and USGS (U.S. Geological Survey). 2005. National hydrography dataset plus, NHDPlus, version 1.0. USEPA and USGS, Washington, D.C. Available: www.horizon-systems.com/nhdplus/. (June 2012).

USGS (U.S. Geological Survey). 2006. National elevation dataset. USGS, Reston, Virginia. Available: ned.usgs.gov/. (June 2012).

USGS (U.S. Geological Survey). 2008. Multi-resolution land characteristics consortium: national landcover database. Available: www.mrlc.gov. (January 2013).

Utz, R. M., R. H. Hilderbrand, and R. L. Raesly. 2010. Regional differences in patterns of fish species loss with changing land use. Biological Conservation 143:688–699.

Waddle, J. H., R. M. Dorazio, S. C. Walls, K. G. Rice, J. Beauchamp, M. J. Schuman, and F. J. Mazzotti. 2010. A new parameterization for estimating co-occurrence of interacting species. Ecological Applications 20:1467–1475.

Wang, L., J. Lyons, and P. Kanehl. 2003. Impacts of urban land cover on trout streams in Wisconsin and Minnesota. Transactions of the American Fisheries Society 132:825–839.

Wang, L., J. Lyons, P. Kanehl, and R. Bannerman. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28:255–266.

Waters, T. F. 1983. Replacement of Brook Trout by Brown Trout over 15 years in a Minnesota stream: production and abundance. Transactions of the American Fisheries Society 112:137–146.

Waters, T. F. 1999. Long-term trout production dynamics in Valley Creek, Minnesota. Transactions of the American Fisheries Society 128:1151–1162.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the USA 108:14175–14180.

Wenger, S. J., J. T. Peterson, M. C. Freeman, B. J. Freeman, and D. D. Homans. 2008. Stream fish occurrence in response to impervious cover, historic land use, and hydrogeomorphic factors. Canadian Journal of Fisheries and Aquatic Sciences 65:1250–1264.

Young, K. A., J. B. Dunham, J. F. Stephenson, A. Terreau, A. F. Thailly, G. Gajardo, and C. Garcia de Leaniz. 2010. A trial of two trouts: comparing the impacts of Rainbow and Brown Trout on a native galaxiid. Animal Conservation 13:399–410.

Zimmerman, J. K. H., and B. Vondracek. 2007. Brown Trout and food web interactions in a Minnesota stream. Freshwater Biology 52:123–136.

Zipkin, E. F., E. H. C. Grant, and W. F. Fagan. 2012. Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. Ecological Applications 22:1962–1972.