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Research Article

A Meta-Analysis of Forest Age and Structure Effects on Northern Flying Squirrel Densities

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ABSTRACT Research on the impact of clearcut logging and partial harvesting practices on northern flying squirrels (*Glaucomys sabrinus*) has shown inconsistent and contrary results, limiting the use of this species as a management indicator species. Much of this variability in study results is due to the labor intensive nature of studying flying squirrels, resulting in small sampling sizes (average = 5.2 sites, $n = 14$) and high variation (CV = 0.59) across studies. We conducted a meta-analysis of relevant studies from North America to determine how forestry practices affect flying squirrel abundance. Mean effect size was -1.18 ($P < 0.001$; $n = 14$) for all studies, indicating a strong difference between control stands and those regenerating postclearcut or following partial harvesting. Our results support the association of northern flying squirrels with mature, uncut forest and their suitability as ecological indicators of these vegetation types.

KEY WORDS experimental power, forestry, *Glaucomys sabrinus*, meta-analysis, partial harvesting, sample size, snags.

Maintaining and monitoring components of biodiversity is a difficult challenge in forested landscapes, especially in light of limited fiscal resources. One approach that has received considerable attention is the use of select species as indicators of ecosystem function and health (Lindenmayer et al. 2002). The northern flying squirrel (*Glaucomys sabrinus*) has been used as an indicator species in many jurisdictions of the United States and Canada (McLaren et al. 1998, Carey 2000*a*; Smith et al. 2005). The northern flying squirrel is considered a keystone species in forested ecosystems because it is an important disperser of hypogeous mycorrhizal fungi (Maser et al. 1978, North et al. 1997). Fruiting bodies (commonly called truffles) of hypogeous fungal species are produced below ground, and because they have no independent means of liberating spores, truffles rely on external agents for spore dispersal. Northern flying squirrels are of particular interest because not only do hypogeous mycorrhizal fungi comprise a large portion of their diet, but the availability of fungi also may regulate their populations (Waters and Zabel 1995, Carey et al. 1999, Currah et al. 2000, Vernes et al. 2004). Flying squirrels potentially become the primary vector for inoculating new areas after disturbances or contributing new genetic material to existing mycorrhizae (Maser et al. 1978). In addition, northern flying squirrels are the dominant prey item for the threatened spotted owl (*Strix occidentalis*).

Northern flying squirrels are thought to be resource- and dispersal limited. Densities of both owls and squirrels are linked to structural features common in old forests such as large-diameter downed woody debris, snags, and tall trees (Rosenberg and Anthony 1992, Witt 1992, Carey et al. 1999, Smith et al. 2004, Holloway and Malcolm 2006). Clearcut logging immediately removes suitable habitat, at least in the short term because northern flying squirrels rarely occur in stands lacking full canopy closure. Moreover, clearcuts also act as dispersal barriers to flying squirrel movements at the landscape scale (Waters and Zabel 1995, Carey 2000*a*, Smith et al. 2011). The gliding locomotion of flying squirrels is unsuited to moving across non-forested vegetation types (Nupp and Swihart 2000; Scheibe et al. 2006; Flaherty et al. 2008, 2010), which may inhibit abilities to traverse openings and may decrease dispersal rates making small populations more vulnerable to local extinction.

Despite their association with old forest characteristics, previous research on the impacts of forest harvesting practices (including clearcut logging, partial harvesting, and thinning) is inconsistent. Half the studies conducted have demonstrated no significant difference in northern flying squirrel abundance in control stands compared with harvested treatment stands (Rosenberg and Anthony 1992; Cote and Ferron 2001; Ransome and Sullivan 2002, 2003; Ransome et al. 2004; Gomez et al. 2005; Lehmkuhl et al. 2006), whereas, the other half have found strong significant negative differences both for clearcutting and shelterwood harvesting compared with controls (Carey et al. 1992; Carey 1995, 2000*b*; Waters and Zabel 1995; Holloway and Malcolm 2006; Herbers and Klenner 2007). We define controls as either naturally regenerating stands that have never been harvested or old forest stands (>100-yr old) in which there has been no selective harvesting activity for ≥50 yr. Treatment stands consist of young second-growth stands (those regenerating postclearcut logging), or stands in which partial harvesting (understory thinning, uniform partial cuts, and shelterwood harvesting) has occurred. Some of

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the variation observed among studies results from differences in retention of old forest legacies (i.e., snag and cavity tree retention guidelines) or harvest intensity.

Trapping northern flying squirrels is labor intensive, requiring large trapping grids (often >10 ha; Carey et al. 1991). This species has a large home range size (typically >5 ha) relative to its body size (Holloway and Malcolm 2007*a*, Smith 2007). In addition, northern flying squirrels tend to be trap-shy (capture rates averaging 0.019–0.030 per 100 trap nights; Smith and Nichols 2003), with recapture probabilities about half that of initial capture probabilities and greater heterogeneity in capture probabilities compared to other small mammals (Smith and Nichols 2003, Hammond and Anthony 2006). Consequently, past research has generally been hindered by small sample size, and the high variation in northern flying squirrel trapability reduces the power of studies to detect significant patterns and generalize study results. In applied ecology and wildlife management, it is crucial to be able to extrapolate the outcome of research studies to broader areas (Guvevitch and Hedges 1993). To increase sample sizes (and thus increase statistical power) and extrapolate existing research to broader areas, we conducted a meta-analysis of studies investigating the influence of harvesting practices on northern flying squirrels from North America.

Meta-analysis is a powerful tool used to understand an entire body of research by analytically synthesizing results of numerous independent studies (Guvevitch and Hedges 1993). Meta-analysis is widely used in other research disciplines (e.g., medicine) and is experiencing increasing use in ecology (Jactel and Brockerhoff 2007, Molloy et al. 2009, Paillet et al. 2010). Meta-analysis offers the advantage of providing quantitative methods, compared with the qualitative summaries that have been traditionally used. Meta-analysis shares the weaknesses of all summary or review methods, but these can be ameliorated with careful selection of studies to include and with consideration of potential study interdependence (Arnqvist and Wooster 1995). Meta-analysis is particularly useful in examining the general patterns of treatment effects in ecological studies that address similar questions and facilitates further insight into how consistent a particular effect is across different study areas (Guvevitch and Hedges 1993, Bengtsson et al. 2005). Meta-analysis provides a quantitative measure of the magnitude of the treatment effect (effect size), which accounts for unequal reliability among studies (i.e., studies with small sample sizes have lower statistical power than studies with large ones; Arnqvist and Wooster 1995, Paillet et al. 2010).

We conducted a meta-analysis of 14 studies that compare northern flying squirrel abundance in control stands with abundance in stands in which timber harvesting has occurred. Our goal was to investigate how northern flying squirrel abundance is affected by forestry practices that influence stand structure. We tested the following hypotheses: 1) northern flying squirrel abundance was similar between old and second-growth stands (long-term effects of clearcutting) and 2) northern flying squirrel abundance was unaffected in the short term (<10 yr) by partial harvesting (i.e., shelterwood, uniform partial cut, or thinning).

METHODS

We performed a search on the Institute for Scientific Information (ISI) Web of Science to collect all papers published on northern flying squirrels. From this search, we selected 14 studies that directly focused on the influence of forestry activities (defined below) at the site level and included all of the required data (mean, standard deviation, and sample size; Appendix). These studies compared estimates of flying squirrel population size (captures/100 trap nights or density [squirrels/ha]) in control stands with harvested stands; hereafter, we refer to northern flying squirrel population data as abundance. Eight of the studies (no. 1, 2, 3, 5, 7, 8, 11, and 12 in Table 1) required no changes to the data because mean, standard deviation, and sample size were directly available; for the remaining studies, we calculated pooled means and pooled standard deviation across study years or sites.

The selected studies focused on 2 general comparisons of flying squirrel abundance in: 1) old (100 yr to >250 yr) versus second growth (35–75-yr-old postclearcut stands)

Table 1. Effect sizes (±95% CI) and weight for each study we used in our northern flying squirrel (*Glaucomys sabrinus*) meta-analysis of all (n = 14) relevant studies in North America comparing treatment groups (young or partial harvested stands) with the control group (old or uncut stands). In addition, we show the sample size required in both control and treatments groups to detect a true effect (at α = 0.05 and power = 0.9) using 1,000 1-way analysis of variance simulations

	Study	Type	Effect size	95% CI	Wt	Required sample size
1	Carey (1995)	Old vs. second growth	−0.85	−2.16, 0.46	8.9	31
2	Carey et al. (1992)	Old vs. second growth	−2.36	−3.77, −0.94	7.6	5–6
3	Lehmkuhl et al. (2006)	Old vs. second growth	−0.04	−1.42, 1.35	7.9	>100
4	Ransome and Sullivan (2003)	Old vs. second growth	−2.28	−5.25, 0.69	1.7	5–6
5	Rosenberg and Anthony (1992)	Old vs. second growth	−0.78	−2.08, 0.52	9.1	37
6	Waters and Zabel (1995)	Old vs. second growth	−1.12	−2.65, 0.4	6.6	18
7	Witt (1992)	Old vs. second growth	−2.76	−4.2, −1.32	7.4	3–4
8	Carey (2000*b*)	Uncut vs. harvested (thinning)	−1.79	−2.97, −0.6	10.9	7–8
9	Cote and Ferron (2001)	Uncut vs. harvested	−0.07	−1.31, 1.17	9.9	>100
10	Gomez et al. (2005)	Uncut vs. harvested (thinning)	−0.34	−1.73, 1.06	7.8	>100
11	Herbers and Klenner (2007)	Uncut vs. harvested (uniform partial cut)	−3.04	−5.06, −1.02	3.7	6–7
12	Holloway and Malcolm (2006)	Uncut vs. harvested (shelterwood)	−1.6	−2.76, −0.45	11.5	9
13	Ransome and Sullivan (2002)	Uncut vs. harvested (thinning)	−0.97	−3.16, 1.21	3.2	23
14	Waters and Zabel (1995)	Uncut vs. harvested (shelterwood)	−2.5	−4.48, −0.52	3.9	5

forests (Table 1); and 2) uncut (>50 yr since any logging activity) versus partially harvested (<10 yr since shelterwood logging, uniform partial cut, or thinning activity) stands. Because 2 studies on the effects of understory thinning sampled different harvest intensities (Ransome and Sullivan 2002, Gomez et al. 2005), we only used the results of the heavy intensity thinning treatments from those studies. The reduction in tree cover (measured as tree density or basal area) in shelterwood or uniform partial cuts averaged 42% (range 6–64%), and 70% (range 43–88%) in stands with thinning. We expect larger effect sizes in studies with shelterwood or uniform partial cuts because of the higher rate of tree removal (particularly mature trees and snags).

We conducted analyses with the METAN (Harris et al. 2009) and METAREG (Harbord and Higgins 2009) modules in STATA 10 (Stata Data Analysis and Statistical Software, Release 10, StataCorp LP, College Station, TX). The base metric in meta-analysis is the effect size (Hedge's *d*), which is the standardized difference between the mean of 2 groups or treatment types, calculated in each study (Guvevitch and Hedges 1993) as:

$$d = \frac{X^C - X^E}{S} J \quad (1)$$

We compared mean abundance of flying squirrels in control stands (old or uncut; X^C) and in experimental stands (second growth or partially harvested; X^E). We divided the difference in means by the pooled standard deviation (S) as:

$$S = \sqrt{\frac{(N^C - 1)(S^C)^2 + (N^E - 1)(S^E)^2}{N^C + N^E - 2}} \quad (2)$$

We then multiplied effect size by a correction factor (J; equation. 3) that accounts for small sample-size bias, calculated as:

$$J = 1 - \frac{3}{4(N^C + N^E - 2) - 1} \quad (3)$$

where N^C and N^E equal the sample size in the control and treatment groups, respectively. The effect size became the difference in standard deviation units between the control and experiment groups.

We then combined effect sizes across all studies using the fixed effects model to estimate average magnitude of effects across all studies (grand mean effect size [d_{++}]):

$$d_{++} = \frac{\sum d_{ij} wij}{\sum wij} \quad (4)$$

where d_{ij} equals the effect size of study *j*, and w_{ij} equals the weight assigned to each study *j* and is calculated as $1/v_{ij}$ from equation 5 below where v_{ij} is the effect size variance:

$$v_{ij} = \frac{N_{ij}^C + N_{ij}^E}{N_{ij}^C N_{ij}^E} + \frac{d_{ij}^2}{2(N_{ij}^C + N_{ij}^E)} \quad (5)$$

A negative value of *d* indicates flying squirrel abundance is lower in second-growth or partially harvested stands than in old or uncut stands. We consider the effect statistically significant if the bootstrapped confidence intervals (based on 999 iterations) do not overlap zero.

Publication bias can be a common problem with meta-analyses because significant results are disproportionally published (Rosenberg 2005). We tested for a publication bias by using Rosenberg's (2005) fail-safe calculator to calculate the fail-safe number for the grand overall effect size, which represents the number of non-significant unpublished or missing studies that would be needed to overturn a significant result. We consider the meta-analysis results robust if the fail-safe number is $>(5n + 10)$, where $n =$ the number of studies in the meta-analysis.

We performed meta-regression to examine the relationship of sample size and large snag density on the study effect size (Sterne et al. 2001). Our objective was to determine if studies with more samples (i.e., more likely to have more precise estimates) were more likely to demonstrate a strong influence of forestry practices and if retention of large snags in treatment stands reduced the observed effect size between treatment and control replicates. The latter is effectively a test of whether snag retention in treatment stands mitigates the effect of other differences in stand structure on flying squirrel abundance. In those analyses, we averaged the control and treatment group sample sizes and used density (stems/ha) of large snags recorded in treatment stands. Large snag density was defined as trees >40 cm diameter at breast height in most studies, except by Holloway and Malcolm (2006), who used >25 cm diameter at breast height. Large snag density has been reported as a potential limiting factor by many authors (Holloway and Malcolm 2007*b*, Smith and Nichols 2003, Smith 2007).

Finally, we used the SIMPOWER (Mitchell 2009) module in STATA 10 to simulate the sample size needed to detect a true effect for each individual study comparing control and treatments groups. The program performs 1,000 1-way analysis of variance (ANOVA) simulations using the sample size, means, and standard deviations of the observed data to perform the power simulation. For this analysis, we set alpha = 0.05, and beta = 0.1 (power = 0.9).

RESULTS

Northern flying squirrel abundance was significantly reduced by forestry practices that influenced the structure or age of residual stands, both in the short and longer term. The overall mean effect size was −1.18 and was significantly different from zero ($P < 0.001$; Fig. 1). An effect size >0.8 is considered large; an effect size of >1.0 is huge (Guvevitch and Hedges 1993). Moreover, the bootstrapped 95% confidence interval (−1.56, −0.79) did not include zero. Comparing old-forest stands with young second-growth stands, the effect size remained very large ($d = -1.18$, $P = 0.005$, 95% CI = −1.80, −0.63). Moreover, northern flying squirrel abundance in partially harvested areas was also reduced compared to uncut stands ($d = -1.18$, $P = 0.005$, 95% CI = −1.76, −0.64). The fail-safe number for the overall grand effect size was 194, which greatly exceeds the threshold used by Rosenberg (2005; here $5n + 10 = 90$) and thus increases the confidence of our meta-analysis results.

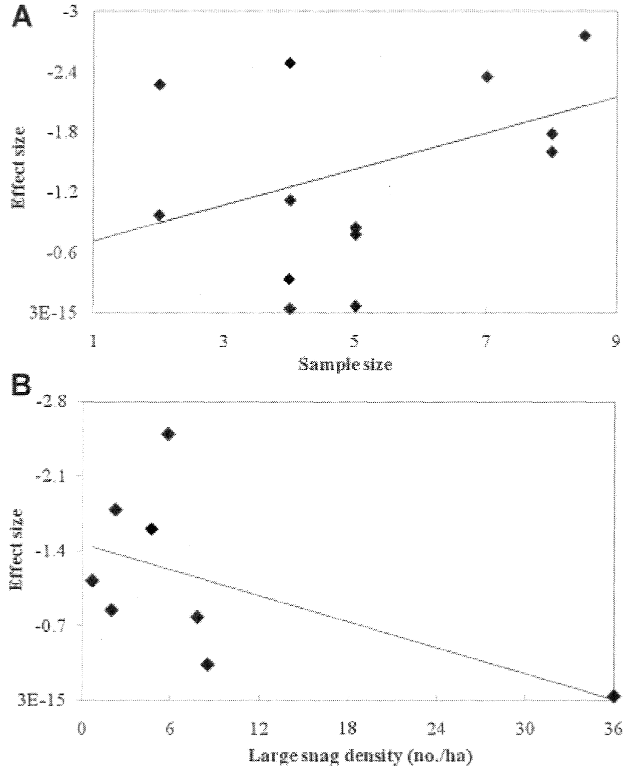

Figure 1. Relationship between meta-analysis effect size from all relevant (n = 14) studies of northern flying squirrel (*Glaucomys sabrinus*) population response to forest management across its range and: (A) averaged sample sizes of control and treatment groups and (B) density of large snags (no./ha) reported for the treatment stands.

Effect size appears to be strongly related to sample size ($P = 0.034$; Fig. 1A). Studies with a sample size of $\geq$6 in both control and treatment groups consistently demonstrated the highest effect sizes. Coincidently, several of the studies with the highest effect sizes also had both the largest samples sizes and a high expectation of strong differences between the control and treatment (i.e., shelterwood or uniform partial cuts). In addition, the 1-way ANOVA simulation of sample size needed to detect a significant difference between the observed data in control and treatment stands showed that 6 is a reasonable minimum sample size based on the power analysis (Table 1). For 5 of the 6 studies reported, significant differences approached or exceeded this minimum sample size.

Finally, summarizing effect sizes may also provide insights regarding factors that limit flying squirrel populations. For example, in our study the highest effect sizes are associated with studies that reduce large snag density to very low levels (<8 snags/ha; $P = 0.131$; Fig. 1B).

DISCUSSION

Our study is one of the first to quantitatively synthesize a body of ecological research that seeks to explain the relationship between forest age and structure and wildlife abundance. Results of our meta-analysis clearly demonstrate that forestry practices negatively influence northern flying squirrel abundance with both short- and long-term consequences. Immediate impacts are seen under partial harvesting practices with frequent return intervals (typically 10–20 yr), such as shelterwood logging and thinning, whereas long-term effects are evident in the reduced suitability of stands that regenerate following clearcut logging, even after 60 yr (Carey 1995). Stand attributes such as snag and tree density, understory plant diversity, and truffle biomass are considered key drivers of northern flying squirrel populations (Carey 1995, Lehmkuhl et al. 2006) and are reduced by stand management activities (Carey et al. 1997, 1999; Carey 2000*a*,*b*; Holloway and Malcolm 2006). In particular, a decrease in snag density is often hypothesized as an important factor driving northern flying squirrel decline (Witt 1991; Carey et al. 1997, 1999; Smith et al. 2004; Holloway and Malcolm 2006). Snags are important for reproductive females as natal cavities and during the winter as den sites (Gerrow 1996, Carey et al. 1997, Cotton and Parker 2000, Smith et al. 2004, Holloway and Malcolm 2007*b*).

Although the regression was not statistically significant, our meta-analysis revealed there may be a snag density threshold below which managed forests are unable to sustain northern flying squirrel populations. Indeed, several investigators reported a positive relationship between snag density and either reproductive female or overall population density (Smith 2007). Smith et al. (2005) reported a 3-fold increase in the odds of capturing northern flying squirrels with every unit (10/ha) increase in large trees or snags, which also explained 65% of variation in population density across study sites. Whether the threshold is actually 8 snags/ha, as suggested from our analysis (Fig. 1B), is not as important as recognizing that cavities are a limiting resource for northern flying squirrels. Consequently, we strongly urge land managers to consider this finding in planning habitat restoration or stand management to enhance northern flying squirrel populations. However, we believe general recommendations for minimum snag size are beyond the scope of our paper. Minimum snag sizes are specific to biomes and ecological communities (Smith 2007), and prescriptions already exist in various portions of this species' range. Additional manipulative experiments or monitoring can be used to evaluate or refine specific management prescriptions across different ecosystems.

Our meta-analysis highlights the importance of understanding the precision of results in a hypothesis-testing framework and in the inferences drawn. Insufficient statistical power in the study design will lead to Type II errors, which bias conclusions that can misguide management responses and lead to wildlife population declines. Failure to reject a null hypothesis of no difference between control and treatments leads managers to conclude the indicator species is not impacted, and thus no management actions are needed (Steidl et al. 1997). Power analyses need to be conducted prior to implementing studies to ensure an appropriate sampling regime is in place to adequately address research objectives and discern biologically significant effect sizes. Power analyses will also enable accurate and reliable statistical judgments to be reported. Meta-analysis results can also be of value here, providing insights into the number of treatment replicates needed in new studies (Arnqvist and Wooster 1995). Our results suggest that $\geq$6 replicate sites are needed in each treatment (6 control and 6 in each treatment type).

Comparing the findings of multiple studies is fundamental to science; indeed, single studies are worth little if not viewed in the context of other similar research (Arnqvist and Wooster 1995). Meta-analysis can be an objective tool to derive robust ecological conclusions from the findings (often inconsistent) of several studies and to synthesize credible generalities to guide more effective species and ecosystem management. Meta-analysis has an important advantage over qualitative summaries because it assesses how influential individual studies are in the context of the larger body of research and weights each study based on study precision and sample size. Meta-analysis is a valuable tool when: 1) results of individual studies are variable (and often contradictory), 2) the expected effect size is weak, and 3) the sample size of individual studies is limited (Arnqvist and Wooster 1995).

Given the inconsistencies in findings among different vegetation types and localities, a meta-analysis was the only method available to objectively summarize the results of studies investigating the influence of forestry practices on northern flying squirrels and to draw consensus among conflicting studies. Previously, this inconsistency has limited the value of northern flying squirrels as a management indicator species and in studies testing silvicultural practices designed to enhance habitat for cavity nesters (i.e., snag and cavity tree retention guidelines). More importantly, our analysis provides reference points for the development of general theory on snag retention (Arnqvist and Wooster 1995). Arguably, meta-analysis can become the basis for developing specific, robust hypotheses that lead to theory. Meta-analysis is an under-utilized tool in wildlife management; it has been applied successfully in other areas of ecology to develop sound theory on contentious issues (e.g., understanding the consequence of biodiversity loss on ecosystem function; Balvanera et al. 2006) and in providing detailed guidance in specific questions such as designing marine fish reserves (Molloy et al. 2009).

MANAGEMENT IMPLICATIONS

Managers are experiencing greater challenges and increasing demands to provide suitable wildlife habitat across industrial as well as public forestlands. The recent paradigm shift toward using the best available science to guide policy and management decisions is often encumbered with inconsistent and conflicting conclusions about the effects of forest management on wildlife communities. Our study not only provides unambiguous direction (i.e., clear, consistent response across forest biomes) regarding the management of forests for northern flying squirrel populations, but more importantly it illustrates the value of synthesizing data from previous studies to obtain credible, robust conclusions to guide policy and management. Equally important, our analysis underscores the importance of considering the expected effect size of response variables in designing manipulative field experiments. Wildlife and forest ecologists can use the results of our analysis as a guide in determining the number of replicates per treatment required to have sufficient statistical power to discern the effects of treatments on response variables.

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Appendix. Northern flying squirrel (*G. sabrinus*) data we used in a meta-analysis, with sample size (n) and mean abundance and standard deviation for the treatment group (young or partial harvested stands) or control (old or uncut stands). We also list whether each study reported a significant difference comparing control and treatment stands.

	Treatment			Control			
Study	N	$\bar{x}$	**SD**	N	$\bar{x}$	**SD**	**Reported significant difference?**
Carey (1995)	5	0.20	0.22	5	0.50	0.20	Yes
Carey et al. (1992)	6	0.90	0.57	8	1.90	0.28	Yes
Lehmkuhl et al. (2006)	4	1.55	0.77	4	1.58	0.79	No
Ransome and Sullivan (2003)	2	1.07	0.15	2	1.50	0.16	No
Rosenberg and Anthony (1992)	5	1.91	0.41	5	2.32	0.62	No
Waters and Zabel (1995)	4	2.28	0.54	4	3.29	1.15	No
Witt (1992)	5	0.40	0.30	12	2.45	0.85	[a]
Carey (2000*b*)	8	0.50	0.28	8	1.00	0.28	Yes
Cote and Ferron (2001)	5	1.01	1.56	5	1.14	2.46	No
Gomez et al. (2005)	4	0.77	0.59	4	0.96	0.53	No
Herbers and Klenner (2007)	10	2.30	0.95	2	5.80	2.26	Yes
Holloway and Malcolm (2006)	7	0.09	0.19	9	0.44	0.24	Yes
Ransome and Sullivan (2002)	2	0.37	0.40	2	0.70	0.27	No
Waters and Zabel (1995)	4	0.36	0.35	4	3.14	1.54	Yes

[a] Did not test for significant differences.