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Elevation, habitat structure and Monteverde bird communities

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ABSTRACT

One hypothesis for why "biodiversity begets biodiversity" when this pattern is observed in bird communities is that by increasing vegetative complexity finer niche partitioning is allowed for among bird species. Bird diversity has been shown to correlate positively with vegetation structure along a successional gradient. However, no such studies have been done in actively managed areas in the tropics. I used three 50 m fixed-radius point counts each in two pairs of study sites at different elevations to compare bird diversity in structurally simple and structurally complex pastures at two different elevations in Monteverde, Costa Rica. Within each pair, one site was simple and the other complex. I measured diversity within and across study sites using a variety of indices. I found that the total number of birds, species diversity, Margalef's index, and the Shannon-Weiner index were all highest in the low elevation site with high structural complexity. These measures were lowest at the lower elevation site with low structural complexity, and intermediate at the two higher elevation sites, which showed no significant pattern. Additionally, I found that the two structurally complex sites were most similar in terms of diversity. This information leads me to conclude that vegetative structural complexity was a more important factor in determining bird diversity than altitude. This provides more evidence to support the "diversity begets diversity" hypothesis when one considers that structural diversity leads to increased resource diversity and feeding opportunities for bird populations.

RESUMEN

Una hipótesis del porque "biodiversidad engendra biodiversidad" cuando se observa este patrón en comunidades de aves es que al aumentar la complejidad vegetativa se permite una partición de nicho más fina entre las especies de aves. La diversidad de aves se ha mostrado correlacionada positivamente con la estructura de la vegetación a través de gradientes sucesionales. Sin embargo, ninguno de estos estudios se ha realizado en áreas activamente manejadas en los trópicos. Yo utilicé tres puntos de conteo de 50 m de radio cada uno en dos pares de sitios de estudio a diferentes elevaciones para comparar la diversidad de aves en pastos estructuralmente simples y complejos a dos diferentes elevaciones en Monteverde, Costa Rica. En cada par, un sitio fue simple y el otro complejo. Medí la diversidad dentro y entre los sitios de estudio utilizando diferentes índices. Encontré que el número total de aves, diversidad de especies, índice de Margalef y el índice de Shannon-Weiner fueron mayores a baja elevación en el sitio estructuralmente complejo, e intermedio en los dos sitios de mayor elevación, lo cual muestra un patrón no significativo. Además, encontré que los dos sitios estructuralmente complejos son más similares en términos de diversidad. Esta información me lleva a la conclusión que la complejidad estructural vegetativa es un factor más importante para determinar la diversidad de aves que la altitud. Esto provee más evidencia para soportar la hipótesis de que "biodiversidad engendra biodiversidad" cuando uno considera que diversidad estructural ayuda a aumentar la diversidad de recursos y las oportunidades de alimentarse para las poblaciones de aves.

INTRODUCTION

Monteverde, Costa Rica, is one of the most biodiverse communities in the world. It contains rich assemblages of many species, but one of the richest is its bird community.

Within the Monteverde region, there are over 450 species, over 200 of which breed in the region (Young and McDonald 2000). The Monteverde area also has a very high level of local variation within the region, making this an excellent area to study patterns of biodiversity.

Two causes of variation in bird communities in the Monteverde area are altitude and vegetative structure. This high variability results in many diverse habitat types being available. Altitude is frequently the most commonly attributed factor to variation in bird diversity in the Monteverde area, largely because of its six Holdridge life zones, each which contains bird communities with diverse assemblages, and is positively associated with altitude. For example, the middle-elevation Pacific Premontane Wet zone contains 6 unique species, while the higher-elevation Lower Montane Rain zone contains 11 (Young and McDonald 2000). Structure has also been examined as a mechanism for diversity in the Monteverde area. Latham conducted bird point counts across a successional gradient with structural complexity that increased from regrowing pasture to secondary forest and primary forest, and found that diversity was strongly positively correlated with both canopy height and foliage height diversity (Latham 1998).

An explanation for this variation of richness in bird communities is that their resource base varies correspondingly, which is known as the hypothesis that "diversity begets diversity." One such study involved ant wrens in Amazonian rainforests. It found that up to 10 species coexisted in the same patch of rainforest via niche partitioning, and then compared the niches they used with the number of niches used by a comparable temperate foraging guild. It further found that several of these feeding niches were unique to the tropics because the structures they relied on were either only present in the tropics or were only available seasonally in temperate zones, preventing specialization. For example, one species foraged exclusively on dead leaves caught in branches, a niche found exclusively in the wet tropics because deciduous forests lack a continuous supply of dead leaves to be caught. Likewise, another ant wren that foraged by gleaning lianas also enjoyed a niche found exclusively in the tropics, because temperate forests have very few such vines (Terborgh 1992).

It is likely that structurally rich communities can support more diversity because it allows for more diverse resource types to be present. In addition to providing more foraging niches that do not overlap and allow for more specialization, it allows many more opportunities for other behaviors such as nesting and predator avoidance as well. According to this pattern, it seems that greater structural diversity should positively relate to greater resource availability (in the form of foraging opportunities, predator avoidance, and nesting resources).

Despite being renowned for its diversity, Monteverde has experienced fairly high levels of human alteration, primarily in the form of clearing forest for cattle grazing, which has led to reductions in structural and resource diversity. Structural reduction varies across a gradient, with extremes present on both ends. Studying the diversity in these extremes allows one to examine the role of moderate reduction in structural diversity as compared to greatly reduced structural diversity as it relates to biodiversity and the diversity begets diversity gradient. Following the studies of Terborgh, any degree of structural simplification will reduce the available resources and number of niches present. This was exactly what was found in a pastureland study in Sweden (Sönderström 2001). However, no such study has been done in tropical regions, which have greater structurally diversity and greater species richness. Perhaps examining the relationship between structure and biodiversity here could lead to more evidence that "diversity begets diversity."

An additional reason to examine pasturelands around Monteverde is that most previous studies of bird diversity in this area have largely examined forest or successional habitats that are not being actively used by humans. However, pastures are a common habitat type in the area around Monteverde and represent no less than 50 of available habitat (personal observation). Since they are so dominant, it is important to understand their effects on local ecology and biodiversity.

In addition to increasing knowledge about the patterns of biodiversity in Monteverde, examining bird species diversity in Monteverde pastures could also have conservation implications. While many farmers interested in creating or expanding pastures do not prioritize planning for any conservation, evidence of a strong correlation between retained structure and species diversity would still be important information to conservation planners from the perspective of range improvement. Windbreaks and the planting of native grass species have successfully improved productivity of many pastures in the Monteverde area, thanks largely to organizations such as the Monteverde Conservation League. The same could be applied to tree structure retention if it is shown to positively correlate with bird abundance.

This study examined the effects of vegetative structural complexity and altitude on bird diversity in four study sites in the Monteverde area. It used two pairs of sites, one at higher elevation and one at lower elevation. Within each pair, one site was structurally simple while the other one was complex. I predict that bird communities in Monteverde pastures will positively correlate with vegetative structural complexity. However, I make no predictions as to whether altitude or vegetative structure will have the greater effect, because I have found no studies addressing this.

MATERIALS AND METHODS

Study Sites

I selected two pairs of study sites; one pair was lower in elevation and was located in the Cañitas area, while the other was higher elevation and located near the Monteverde Cloud Forest Preserve. Within each pair of sites, one site was in a completely open pasture, while the other pasture had a retained overstory of large canopy trees. Table 1 summarizes exact location data.

TABLE 1. *Description of each study site. All location measurements were taken with a handheld Magellan SporTrak Pro ® GPS unit.*

Site Name	Region	Structure	Lat (°N)	Lon (°W)	Alt (m)
ALB	Cañitas	Simple	10.32466	84.84502	~1350
VJT	Cañitas	Complex	10.32121	84.83540	~1275
BUL	Cloud Forest	Complex	10.29640	84.80131	~1500
MAR	Cloud Forest	Simple	10.29705	84.80423	~1475

The pair of study sites in the Cañitas was located in the Pacific Premontane Wet life zone, as classified by the Holdridge system. Before the 20th century, much of this area was forested, but much of it has now been cleared for dairy farming, coffee production, and rural housing. The higher elevation study sites, by contrast, were located in the area immediately north and west of the Monteverde Cloud Forest Preserve. This area is classified as Lower Montane Wet, according to the Holdridge system. Much of the area to the east is primary and secondary forest that is protected in the Monteverde Cloud Forest Preserve and the Children's Eternal Rainforest (Fogden 1993).

In the Cañitas area, one site was located on the farm of the Victor Torres family. This site was characterized by a moderate elevational gradient, an uneven distribution of retained trees, occasional windbreaks and a few small sun-grown coffee patches (<2 ha each. The canopy structure here was sufficient to facilitate many foraging opportunities and the vegetation considered complex. The other site in the Cañitas area was located on the southeast corner of Alberto Castro's farm. While the Castro farm is very large (>50ha) and highly varied, this particular section was characterized by a steep, east-facing pasture with rocky soil and mostly devoid of vegetation at higher elevations. At lower elevations, several species of trees and shrubs grew in a somewhat stunted form to approximately 8m tall. Many trees exhibited varying degrees of wind-restricted growth, presumably due to a nearly continuous east to northeast breeze. The general lack of vegetation above 1 m tall (with the exception of the few trees mentioned) led this site to be considered structurally simple.

The structurally complex study site near the Monteverde Cloud Forest Preserve was a currently inactive pasture with fairly dense, tall trees in a fairly uniform distribution. There was virtually no vegetation of intermediate height—only a dense herb layer and fairly uniformly aged trees, most approximately 20m tall. The pasture area was fairly small (<5ha) and surrounded on all sides by a dense and structurally complex forest. The structurally simple site was also located in a relatively small pasture (<10 ha) and was characterized by active cattle grazing and fairly widely distributed and nearly leafless trees that supported rich epiphyte communities. Like the closed site, it was surrounded fairly closely by closed forest, but was bordered on one side by the road running between Monteverde and San Luis.

Methodology

Within each of the four study sites, three 50 m, fixed-radius point counts (Ralph et al., 1991) were established, for a total of 12 survey points. Each point was at least 100m from the next nearest point and ideally at least 50m from the edge of the selected habitat type. Each point was visited 5 times from November 2 to November 12, 2008 during the hours of 0600-1100 and 1400-1700. At each point, I counted birds for 10 minutes, recording all stationary birds detected visually or aurally. Birds flying over were noted as well, but were recorded separately.

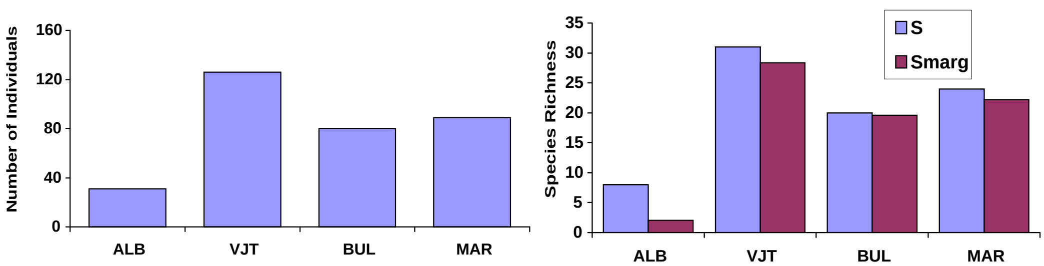
Statistical Analysis

To analyze my findings, I combined all observations from each site into one Excel spreadsheet and tallied the number of individuals found. For each study site, I calculated species richness, number of individuals observed, evenness, Margalef's index and the Shannon-Weiner diversity index. I then graphed each measure across all four study sites to visually compare the results. In addition, I compared the Shannon-Weiner diversity index of each site with all others using Student's paired t-test. Finally, I used EstimateS 8.0 (Cowell 2006) to compare species presence and species abundance distribution across all study sites (calculated with Sorenson's Qualitative and Morisita-Horn indices, respectively).

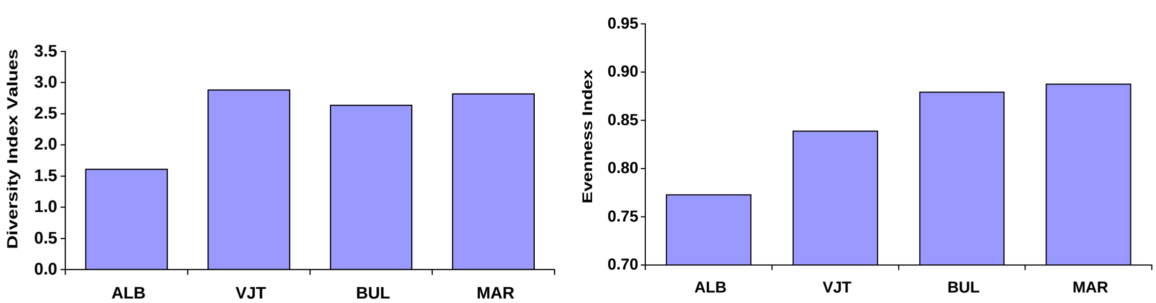
RESULTS

Diversity Information

I observed a total of 49 bird species during my surveys, with 13 additional species seen flying over (see Appendix 1 for complete observations). I found that the lower elevation open site had the lowest number of individuals, while the lower elevation closed had the highest (Fig. 1). Likewise, the lower elevation open site showed the lowest species diversity, Margalef's index, and Shannon-Weiner diversity index, while the lower elevation closed had the highest (Figs 2 and 3, respectively). The higher elevation open had the highest evenness, while the lower elevation open had the lowest (Fig. 4).



FIGURES 1A AND 1B. *Number of species detected at each of four study sites (left), along with species richness and Margalef's index for each of the four study sites (right). Study sites are lower elevation open, lower elevation closed, higher elevation closed, higher elevation open, left to right. Monteverde, Costa Rica, November 2008.*



FIGURES 2A AND 2B. *Shannon-Weiner diversity index for each of the four study sites (left) and evenness index (right). Study sites are lower elevation open, lower elevation* *closed, higher elevation closed, higher elevation open, left to right. Monteverde, Costa Rica, November 2008.*

When a paired t-test was performed to compare the Shannon-Weiner diversity index of each site to the others, the lower elevation open site showed significantly less diversity than its partner closed site, and also less diversity than either of the two other sites ($p<0.5$ for all three comparisons). None of the other pairwise comparisons showed significant differences.

TABLE 2. *Modified t-test of H'. Bold text indicates significance (critical value of t=2.00)*

First Sample	ALB	ALB	ALB	VJT	VJT	BUL
Second Sample	VJT	BUL	MAR	BUL	MAR	MAR
t	**-55.17**	**-5.56**	**-6.61**	-1.78	-0.43	-1.59
df	97.37	48.30	47.44	60.13	63.91	167.88

Finally, I used EstimateS to calculate the Sorenson qualitative index and Morisita-Horn index. I found that the lower elevation open site differed strongly from the closed sites and was more similar to the high elevation site. The closed sites were most similar in terms of diversity, while the lower elevation closed was most similar to the high elevation open in terms of composition (Fig. 5).

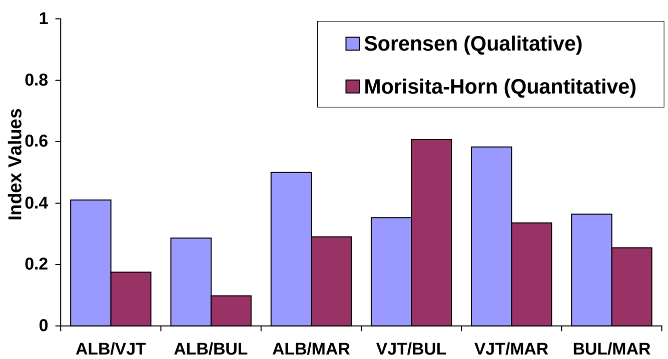


FIGURE 3. *Sorenson qualitative index and Morisita-Horn index comparing bird community composition in each of four study sites with all others, Monteverde, Costa Rica, 2008.*

Species Composition Information

I noted the most common species in each study site and also which species was present in which habitats. I found that Great-tailed Grackles only appeared at the lower elevation sites and Common Bush-Tanagers only appeared at the higher elevation sites. I also found that Wilson's Warblers only appeared in closed habitat types. One species of bird made up almost half of all observations (15 of 31) in the lower elevation open habitat (Yellow-faced Grassquit) and was never observed more than three times in any other site.

DISCUSSION

My prediction that vegetative structural complexity is correlated with bird diversity was supported. I conclude this in two different ways. First, I found a positive relationship between bird diversity and vegetation structure. Second, the composition of specialist species in each habitat type led me to conclude that these habitat types differed from a bird's perspective (in terms of resources such as food and nesting opportunity) as well as structurally.

Diversity Analysis

I used several reasons to conclude that structural diversity correlates strongly with bird diversity. First, the lower elevation site with simple structure had significantly lower bird species diversity than all other habitats, especially the lower elevation complex site both from a visual comparison and from pairwise t-tests. It was also the least structurally diverse of any site. None of the other sites differed significantly according to the t-tests. I also conclude that the diversity of habitats created via greater structural diversity is more important in determining bird diversity that is altitude. If altitude were important, I would expect there to be other significant differences. Additionally, community comparisons showed that the two closed sites were the most similar in terms of diversity.

One reason that the lower elevation closed site may have had the highest diversity was because it had the greatest structure, both horizontally and vertically. While much of the study area was active pasture, it was mixed with small patches of coffee and sugarcane. One of my survey points was near a windbreak, and trees were frequently distributed in clumps and varied in age in several instances. Perhaps this indicates that horizontal structural heterogeneity plays a role in regulating diversity in bird communities around Monteverde by providing opportunities for species that require several structures for different purposes. While these species may forage in the open habitats, they may still utilize grown-over areas such as sugarcane or windbreaks for roosting and predator avoidance. Additionally, the increased heterogeneity may provide more food sources and enable greater niche partitioning. Indeed, Terborgh (1979) found a positive relationship between horizontal structural diversity and bird communities.

While the difference in bird diversity between the lower elevation open and closed sites was large, this difference was much less at the higher elevation sites. In fact, the structurally simpler site had higher measures of diversity than the complex site. There are several possible reasons for this. First, the higher elevation simple site was appreciably more complex than the lower elevation simple one. At this site, there were a fairly high number of trees within the pasture (even though nowhere near enough to form a closed canopy), and while at first glance they appeared to be dead or dying, many of them actually supported some live leaves. Perhaps even more significantly, many of these trees had healthy and diverse epiphyte communities that I observed birds utilizing for foraging, especially hummingbirds. Based on these observations, it appears the moderate level of structural complexity here and associated resources were somewhat intermediate between the low elevation simple site and the complex sites.

Species Composition

Also important in concluding that structure played an important role was the observation that several specialist species occurred only in certain habitats or elevations. Wilson's Warblers, for instance, were the most abundant species in the low elevation complex site and the second-most abundant in the high elevation complex site, but were entirely absent in both simple sites. It is perhaps surprising to observe how common they were, considering they are associated with well-developed understory habitats, which appeared largely absent in any of the pasture habitats I surveyed. Perhaps the fairly complex canopy communities with dense vegetation, lianas, and epiphytes provided sufficient substrate for the insects they feed on. Additionally, none of the points where they were common were more than 100 m from an area with a denser understory. It is possible that they utilize more open areas for feeding but never venture too far from denser understory habitats that offer them a safe retreat when necessary.

I also noticed a similar pattern of abundance with regard to an open-area specialist, the Yellow-faced Grassquit, which was extremely abundant at the lower elevation open site and rare other places. The structural complexity of this site was very low both horizontally and vertically with only a few small, stunted trees in a pasture of uniformly distributed grass clumps that appeared to be of a single species. Some studies show that open habitat specialists like grassquits (Stiles and Skutch 1989) actually show a negative correlation between abundance and structural diversity (Laiolo 2004). This appeared to be the case here, and could be due to the fact that grassquits get all their necessary resources from open fields. They feed on grass seeds, nest in dense grass, and use it for predator avoidance as well (Stiles and Skutch 1989, pers. obs.).

Even with evidence to conclude that there is a relationship between vegetation structure and bird diversity, altitude and/or metacommunity appears to have some effects as well, especially on species composition. For example, Common Bush-Tanagers were the most common species in the high elevation closed site and were also present in the open site, but were completely absent from both lower sites. They feed primarily on berry-producing epiphytes, which were far more common at high elevations, and might explain the birds' distribution. Likewise, Great-tailed Grackles, which are associated with human activity, were present at both lower sites, but absent from both upper sites.

Additional Results/ Future Study

One explanation for the higher diversity in the higher elevation open site as compared to the closed site is that the forest surrounding the pasture was influencing the open site. The high elevation closed site was also a fairly small habitat patch, and it may have been experiencing these effects as well (I did indeed detect several closed forest specialist species here, Stiles and Skutch 1989). However, this contrast was much greater in the open habitat, possibly leading to a more pronounced effect. One final explanation for the higher diversity in the higher elevation open habitat was that it was simply difficult to observe birds in the closed habitat. Many birds passed through unidentified, flying from closed forest on one side of the pasture to closed forest on the other and only pausing briefly in between.

In considering improvements for future studies, a quantitative investigation would provide stronger evidence of the connection between habitat diversity and bird diversity. A second reason for a quantitative study is that it proved very difficult to find study sites that fit the description of "completely open" or "completely closed canopy." Hence, it would probably be more useful to select a gradient of study sites at each altitude and attempt to numerically correlate vegetative structural complexity with bird diversity.

Finding that bird diversity in pasture habitats is positively correlated with vegetation structure suggests a relationship between structural diversity, resources that birds use (e.g. food resources), and the birds themselves. It also provides more evidence for the hypothesis that diversity begets diversity across many different habitat types. In addition, it provides an argument for conservation of vegetative complexity in pastures and also may provide a new route for farmers seeking to improve habitat quality in their pastures.

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APPENDIX 1. *Summary of point count observations. "F" denotes a flyover bird; flyovers were not used in the analysis. Numbers in cells refer to the number of non-flying birds observed in each habitat. Site codes were as follows: ALB=lower elevation with simple structure, VJT=lower elevation complex, BUL=higher elevation complex, MAR=higher elevation simple.*

Species	ALB	VJT	BUL	MAR	Total
Black Vulture	F	1	F	F	1
Turkey Vulture	F	F		F	F
Broad-winged Hawk			2		2
Short-tailed Hawk	F				F
Rock Pigeon		F			F
Red-billed Pigeon		2			2
Ruddy Pigeon		F			F
Crimson-fronted Parakeet		F	F		F
Parakeet sp.				F	F
Brown-hooded Parrot				15	15
White-fronted Parrot	F	2		7	9
Vaux's Swift				F	F
Green Violet-Ear			4		4
Stripe-tailed Hummingbird				1	1
Hummingbird sp.	F	1	3	2	6
Coppery-headed Emerald				1	1
Magenta-throated Woodstar			1		F
Emerald Toucanet		F			F
Hoffman's Woodpecker				1	1
Woodpecker sp.		1	1		2
Red-faced Spinetail			1		1
Streak-headed Woodcreeper		1			1
Eastern Wood-Pewee	1	4	5	2	12
Dusky-capped Flycatcher		1			1
Boat-billed Flycatcher		2		2	4
Great Kiskadee				1	1
Social Flycatcher	1	2		5	F
Tropical Kingbird		2		3	5
Flycatcher sp.		F			F
Masked Tityra		2		F	2
Yellow-throated Vireo		1			1
Philadelphia Vireo		1			1
Brown Jay	5	1	1	7	14
Blue-and-white Swallow	F	F		F	F
Barn Swallow	F				F
Swallow sp.	F				F
Plain Wren	2	1		1	1
House Wren	3	2	9	6	2F
Gray-breasted Wood Wren			3		3

Slaty-backed Nightingale Thrush			1		1
Clay-colored Robin		1			1
Mountain Robin			3		3
Tennessee Warbler		1			1
Black-throated Green Warbler		8	3	3	14
Black-and-white Warbler		1			1
Wilson's Warbler		21	11		32
Gray-crowned Yellowthroat		1		1	2
Warbler sp.		5	1	1	7
Common Bush-Tanager			14	3	17
Hepatic Tanager			4		4
Blue-gray Tanager		4		5	9
Tanager sp.			1		1
Yellow-faced Grassquit	15	1		3	19
Rufous-collared Sparrow	3	4		12	19
Sparrow sp.				1	1
Eastern Meadowlark				3	3
Great-tailed Grackle	F	11			2
Baltimore Oriole		2			2
Golden-browed Chlorophonia			3		3
White-vented Euphonia		4			4
Unknown sp.	1	8	9	3	21
Total	31	99	80	89	276